# The Wing Venation and Respiratory System of Certain South African Termites.

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With Plates III—XI.

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## REVIEW.

CERTAIN results of this investigation appear to be at variance with usually accepted views on wing-venation, and for the sake of clearness the main features of the present paper are briefly summarised in the following paragraphs:

(1) The series of ribs supporting the termite wings are derived from thickenings of the cellular tissue of the developing organ.

(2) One of these thickenings is in the form of an ambient, and develops independently around the margin, whilst the rest form about tracheæ. Subsequently, that portion of the ambient thickening which extends along the outer margin is converted into the rib costa.

(3) The ontogeny of the tracheæ in a termite wing-sac does not support the generalised scheme of Comstock and Needham, in which all the tracheæ spring from an anterior and posterior trachea arising respectively from the dorsal and ventral longitudinal tracheæ of the thorax.

(4) The tracheæ of the wing-sac develop from two or from three buds forming very early in nymphal life upon each of the four sections of the spiracular trunk tracheæ within the meso- and metathorax and not upon the dorsal and ventral longitudinal trunks.

(5) The position and branching of the longitudinal ribs of the wing are almost wholly dependent upon the position and

development of the longitudinal tracheæ, except in the case of the costa, which is not preceded by a trachea. That the costa is not preceded by a trachea is confirmatory of the views of Fritz Müller, Spüler, Brauer, and Redtenbacher.

(6) From the examination of Calotermes durbanensis *Hav.*, the fundamental or primitive scheme would appear to be for the ribs, Radius, Media, and Cubitus to be associated with the main wing-sac tracheæ which arise separately from one another from the spiracular trunk tracheæ of the thorax.

(7) The variation in the venation, so decidedly characteristic of the termite wing, is chiefly due to the erratic development of the tracheæ of the wing-sac.

(8) The extra principal ribs frequently met with in a termite wing are due to the growth of extra principal tracheæ in the wing-sac.

(9) The specialisation of the wing-ribs, apart from the costa, is one of reduction; first, in the degree of branching, and then in complete atrophy. This is dependent upon a more or less equal reduction in the tracheæ of the wing-sac.

(10) The respiratory system of a newly-hatched termite consists of a framework of comparatively few simple tracheæ, from which a multitude of dichotomising, arborescent, and other tracheæ gradually develop and grow.

(11) The specialisation of the respiratory system is one of reduction, the nascent system of the more specialised termites (Metatermitidæ) being less extensive than is that of the more generalised termites (Protermitidæ and Mesotermitidæ). The principal difference is the presence of a pair of ventral longitudinal trunk tracheæ in the Pro- and Mesotermitidæ and the absence of such in the Metatermitidæ.

(12) The valvular spiracles of the abdomen of an adult termite are derived by gradual transformation from the occluding apparatus of the spiracles with a fixed opening exhibited by the nymphs; and this transformation is more decided in the females than in the males.

(13) The slit-like spiracles of the abdomen of highly distended females (queens) of the Holmgren genera Termes and

Odontotermes represent disruptions of the final valvular spiracles.

## I. INTRODUCTION.

This contribution towards a knowledge of certain Termite features rests upon a number of limited studies of various local species that I have been able to make from time to time. Each study is at best imperfect, because I have been limited by want of opportunity and material; and, further, because the phases of structure and development recorded have been investigated by ready and simple methods of examination. For this latter reason the anatomical details are separated by many lacunæ, gaps that might have been filled at the time had the technique employed been more elaborate. It was not, however, my original intention to pursue the matter as far as I have. With a view to establishing a satisfactory working nomenclature for the ribs of the termite wing, I first turned for guidance to the tracheation of the developing organ, and this led me to examine the general respiratory system. That wing-venation and the tracheal system can be treated together shows how inseparably the two are connected.

As a result, certain independent conclusions had been arrived at, and a radical change made in the accepted nomenclature of the wing-ribs. It is possible that these may bring me into conflict with what is regarded by a large school of modern entomologists as the last word upon the subject; in any case, they invite criticism. Should such criticism lead to a more thorough examination of the termite wing and its ontogeny by others more competent to handle the subject, my efforts will have served a good purpose even if it be shown that, in company with many another isolated observer, I have made some fundamental errors.

It will have been noticed that the supports of the wing are spoken of as ribs, not as "veins" nor as "nervures." On the other hand, the assemblage of these ribs is called venation. The use of either "vein" or "nervure" implies an adherence to one or another school of entomology; from this objection the more homely rib is free. But, in referring to the several supports of the wing as ribs, one should perhaps apply costation to the assemblage. It would be capricious, however, to introduce a new term when venation is so generally employed.

Upon the whole, few new terms have been introduced, and then only to meet special cases or to avoid prolixity. Generally, terms will be found employed in the broad sense of their common acceptance by entomologists or botanists.

The generic and family names used are those of Holmgren's classification.[1] Unfortunately, the specific name of a termite under reference cannot always be indicated; such is referred to the genus or subgenus into which it falls in the classification mentioned. This, together with a desire to avoid a too frequent repetition of the names of recognised species, leads to certain characteristics being described as generic. In every case, however, it is to be understood that any such statement does not involve the genus further than those South African species enumerated in the Appendix.

Sometimes the word "wing" is applied to the developing organ, but, ordinarily, this is spoken of as the "wing-sac."

Except for those that are obviously diagrammatic, the illustrations reproduce some of my many camera-lucida sketches, as faithfully as possible, with a none too facile pen.

It is to be noted, however, that in most cases when the wing-sac of a more or less mature nymph is treated, the basal connections of the principal tracheæ are simplified. In such wing-sacs, after entering the shoulder and thoracic cavity, these tracheæ are profoundly looped; often more so than in figs. 140 and 153 (Pls. IX, X). To reproduce them as they are actually arranged would give a very involved illustration. The loops are, therefore, eliminated and the basal connections shown as they appear in young nymphs.

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[1] Holmgren, Nils. 'Termitenstudien,' parts i. ii. iii; Upsala and Stockholm, 1909, 1911, 1912.

Further, in mature nymphs the median trachea is in contact with either the radial or the cubital in the base of the wing-sac; in the figures it is shown separated.

## II. THE ORIGIN OF WING-VENATION.

The wings of termites seem to be the final form of pouch-like expansions of the meso- and metathorax. Tracheæ are not absent from "the wing fundaments" as has been stated, and the buds, from which later on they develop, certainly form before any thoracic extension is noticeable.

In 1906 Woodworth[1] developed a general theory of wing-venation which suffered criticism because he ignored, or set out to controvert, the accumulated evidence showing the venation of the insect-wing to be derived from the tracheation of the developing organ, or, as he rather sceptically puts it: "The veins simply represent the tracheal arrangement." He argued: "The more rational conception is that there existed at the beginning and has existed through all time to the present day, a mechanical necessity, in accordance with which the primitive venation was produced and all its essential features have been maintained through all the vicissitudes of the ages . . . mechanical necessities are the dominant factor in their (the veins) first production and in their subsequent development." This theory may be said to apply to the ontogeny of wing-ribs described by Lowne,[2] as follows: "The walls of the wing-sac become plicated in fan-like folds, radiating from its attachment to the thorax, the angles of the folds become thickened and form the primary veins."

Whilst the elaboration of Woodworth's theory finds no place here, his suggestion of a marginal vein is important. He says little more than this: "One of the first veins to appear is the marginal. . . . The marginal vein is often not uniform in size around the whole wing, being usually strongest on the front margin, often weak on the hind margin, and quite commonly entirely absent on the outer (distal) edge of the wing." What else is said has but to do with an imagined ontogeny. The point is that the termite wing does possess a marginal rib, which is pronounced along the outer margin and often more or less faded out along the inner; it is, in no conceivable manner, derivable from an immediate or remote tracheal forerunner.

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[1] Woodworth, C. W., "The Wing Veins of Insects." 'University of California, Technical Bulletins,' vol. i, pt. i, 1906.

[2] Lowne, B. T., "The Blow Fly," London, 1890-5.

Among earlier writers, Fritz Müller, Spüler, Brauer, and Redtenbacher claimed that the wing-ribs arose from pre-existing tracheæ except, they held, that the outermost or costa did not have a trachea as its origin and therefore had nothing to do with the "veins." Comstock and Needham,[1] in a very able and convincing demonstration, seemingly succeeded in showing that all the ribs, including the costa, were in the beginning preceded by tracheæ; unfortunately, they give no particulars of their studies of the wing tracheæ of Termites, otherwise I might have found no difficulty in reconciling myself to their view. Their studies enabled them to make the following definite announcement: "It can be accepted as a firmly-established fact that the courses of the wing-veins of primitive insects were determined by the courses of the pre-existing tracheæ." So far as termite wings are concerned, the studies now submitted will show that those ribs that are preceded by tracheæ reflect the courses and developments of those tracheæ; and, the more generalised the wings, the more is the individuality of a pre-existing trachea recorded in the final wing. The studies, however, controvert the doctrine that the costa is also preceded by a trachea.

As one of the main features of their thesis, these authors put forward "a hypothetical type to which the wings of all orders might be referred." They indicated the primitive condition of the basal connections of the wing-tracheæ and devised two routes of specialisation, one of addition, the other of reduction.

The hypothetical type was "represented by the tracheæ which precede the forming veins," and accorded well with the venation of the most generalised wings they presented. All the principal veins are traced to two tracheæ which enter the wing-sac, one on its anterior and one on its posterior border. The anterior is described as "a branch of the dorsal longitudinal trachea," the posterior, "of the ventral longitudinal trachea." Unfortunately, these two tracheæ are not further defined. Such tracheæ are present in our more generalised termites (Hodotermes, Calotermes, Cryptotermes, and Rhinotermes), but the basal connections of the wing tracheæ are far removed from them. According to the type, each of the two wing tracheæ, on entering the wing-sac, subdivided into four principal stems so as to form an anterior and a posterior group. The anterior shows the costal, the sub-costal, and the radial as outer branches of the medial trachea; the posterior shows three anals as inner branches of the cubital trachea. To each principal trachea was given a typical development, some being simple and others variously branched (fig. 1, Pl. III).

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[1] Comstock, J. H., and Needham, J. G., "The Wings of Insects," 'The American Naturalist,' vols. xxxii, xxxiii.

As reflected in the figure, the type was enlarged as follows: "In most insects there has been developed a transverse trachea connecting these two groups of tracheæ. . . . Frequently the transverse basal trachea is indistinguishable from the two main trunks which it connects, the three forming a single, continuous transverse trachea from which arise all the wing tracheæ. . . . When a basal trachea is formed the medial trachea tends to migrate along it towards the cubito-anal group and often becomes united with that group. In some cases the base of the radial trachea tends to follow the base of the medial in its migration along the basal trachea towards the cubito-anal group." This linking up of the two groups of tracheæ (as shown by the dotted lines in the figure) is regarded by the authors as a more specialised condition. Inasmuch as the principal tracheal stems within the wing-sacs of all the termites I have examined are post-embryonic developments from the spiracular trunks[1] and not from the dorsal or ventral longitudinals; and almost invariably issue from these trunks between the arms of the Y-shaped tracheæ of the second and third legs, fig. 48 (Pl. V), there would appear to be little relation between the termite system and that of the hypothetical type. More particularly is this so when it is realised that the ever-present spiracular trunks lie between the dorsal and ventral longitudinal tracheæ, when the two latter are both present. Further, whilst there is some evidence to show that the basal connections of the principal tracheæ tend to migrate in a posterior direction, the trachea which is attached to the base of the cubital in many termite species and which precedes the median rib of the wing is not necessarily a migrant medial trachea. Where this condition occurs, the evidence all goes to show (a) that the medial trachea has disappeared and (b) that there are two principal cubital stems (see, in particular, Microtermes incertus, Section IX *g*).

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[1] See Section V for definition of "spiracular trunk," etc.

The theory of specialisation proposed by the authors (Comstock and Needham) is rather arbitrary. Specialisation by addition takes place only by "a multiplication of the number of the branches of the principal veins," whilst specialisation by reduction follows the atrophy and coalescence of veins. "In nearly every case," they state, "we found the reduction of the pre-anal area accompanied by a similar tendency in the anal area, or, if a reduction has not taken place, there is no increase in the number of veins in this area, the tendency being towards the production of a fewer-veined wing." It is enough for me to add that there is nothing throughout the work under reference bearing upon specialisation by reduction which the ontogeny and final condition of the termite wing does not seem to confirm. But the venation of the termite wing is such that it cannot be derived from the hypothetical type except by methods that are difficult and unacceptable. If anything, the study adds to the palæontological evidence and supports "the quite generally accepted view that the primitive insect wing had many wing veins" (C. & N.)

## III. THE NOMENCLATURE AND NUMBERING OF THE WING-RIBS.

The two systems of naming and numbering now proposed rest upon evidence which will be given in a subsequent section. In introducing them here sequence has been subordinated to other considerations, it being impossible to proceed without a recognisable nomenclature. The notation is secondary to the nomenclature, and is suggested to meet the frequency with which certain principal tracheæ, and, therefore, certain principal ribs are duplicated. Upon the whole both systems indicate that there is no fundamental difference between the venation of the termite wing and the wings of other generalised insects.

O. Costa.—The costa of common acceptance. The term is employed to describe that part of the ambient which is modified into a chitinised and stiff rib for the support of the outer[1] margin of the wing. (Exceptionally, as in the hind wings of Calotermes and Cryptotermes, the costa may be composed of costa and post-costa.)

I, Ia. Post-costa.—This is an obsolete term reintroduced to describe the first auxiliary, a reduced principal rib. The term distinguishes it from the second auxiliary or sub-costa. The post-costal trachea is probably often homologous with the simple costal trachea of Comstock and Needham, where it appears—as in the case of the hind wings of Calotermes and Cryptotermes—to precede the costa.

II, IIa. Sub-costa.—This rib is: (1) the radius of Holmgren; (2) Desneux' principal branch (R. 1) of the radius; (3) Hagen and Sjostedt's branch of the sub-costa.

III. Radius.—This is: (1) the radius of Desneux; (2) the radial sector of Holmgren; (3) the sub-costa of Hagen, Sjostedt, and others. The pre-existing trachea of the rib, in such generalised forms as Hodotermes and Calotermes, very greatly resembles the condition found in the cockroach.

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[1] The termite wing is regarded as possessing only two margins, an outer and an inner.

IV, IVa. Media.—This term is applied, conservatively, to the rib which succeeds an independent medial trachea.

V, Va.—Cubitus.—This is the cubitus or sub-media of general acceptance. It corresponds with the branched Cu. 1 of the cockroach. In the wings of certain species it is duplicated, and then the anterior stem (Va) precedes a sub-median rib, which will be called the pseudo-media, as in certain respects it imitates a true media.

VI, VIa. Anal.—The anal of general acceptance.

Hitherto, the names given to the principal ribs of the termite wing have not been based upon ontogenetic considerations, and this will explain the decided differences in the accompanying table, into which Comstock and Needham's nomenclature has been introduced for purpose of comparison.

Nomenclatures: Table of Comparison.

| Suggested. | Comstock and Needham. | Desneux. | Holmgren. | Hagen and Sjostedt. |
|---|---|---|---|---|
| O. Costa . . | Costa | Costa | Costa | Costa |
| I. Post-costa . | — | Sub-costa | Sub-costa | Sub-costa |
| II. Sub-costa . | Sub-costa | R. 1. | Radius | |
| III. Radius . . | Radius | Radius | Radial sector | |
| IV. Media . . | Media | Media | Media | Media |
| Va. Pseudomedia . | Media | Media | Media | Media |
| V. Cubitus . . | Cubitus | Cubitus | Cubitus | Sub-media |
| VI. Anal . . | Anal | Anal | Anal | Anal |

The earliest of these nomenclatures was probably that of Hagen, and it seems to rest upon the condition of the more specialised wing.

A decided improvement in naming the wing-ribs was introduced by Desneux. He did not recognise Hagen's sub-costa as such but as the radius; and he called the first auxiliary "sub-costa" and the second auxiliary, "the principal branch of the radius," or R. 1.

My own studies of the final tracheal arrangement in Hodotermes, Calotermes, and Cryptotermes led me to at first regard the second auxiliary as the principal branch of the radius, but the following features convinced me that it is a principal: (a) the regularity with which the preceding trachea develops before any normal branches of the radial trachea arise; (b) the coinciding of its branching (when it does branch) with the branching of the radial and other principal tracheæ; (c) the fact that it has occasionally been found in a duplicated condition (in Calotermes); (d) the occurrence of a gradual modification from a branched rib to complete atrophy.

Holmgren attached sufficient importance to this rib to name it the radius; this supports my view that it is a principal. Radius is, however, an unfortunate misnomer for the rib in question, and the application of the term radial-sector to the true radius is inapt.

## IV. THE TERMITE WING.

In being deciduous the termite wing possesses a striking character absent from the wings of all other insects. In text-books it is usually stated of both ants and termites that they "shed" their wings, but the two cases are not analogous. A part of the termite wing is shed, whilst a part is permanently retained. For the permanent part there is no better term than "wing-stump," and to the temporary region (the blade with which the air is sculled in flight) "lamina" is applicable.

These laminæ I regard as documents whereon is embossed in hieroglyphs much of the early history of the termite wing-ribs. It seems to me that the provision for shedding the expanded part is, if not original, indeed very ancient; and that the habit of casting a part was acquired when the venation was in a primitive, unspecialised condition. Hence the laminæ preserve evidence of a condition that must once have prevailed. As a Rosetta stone was needed for the correct interpretation of the writings of Egypt, so only by looking into the development of the wing can the evidence supplied by the venation be unravelled and its significance appreciated.

For the transverse suture that cuts across the base of the wing and sharply defines the wing-stump from the lamina, the term "line of fracture" seems most appropriate, as it is here that the lamina breaks away from the stump when the wing is bent, whether artificially, accidentally, or by the muscular effort of the termite.

The ultimate function of the wing-stump seems to be that of protecting the membranous wing-socket throughout the long life of the imago. According to its extent, or according to the degree to which it is chitinised, it reveals or conceals the basal arrangement of the venation. In some species, therefore, its characters are helpful, in others confusing.

In the majority of species the stumps of all four wings are relatively small and sub-equal; in others, those of the fore-wings are proportionately quite large. The first condition is characteristic of the more specialised termites, the second is only met with among the more generalised; but, as certain of the latter (Hodotermes, etc.), exhibit the first, there is really little to indicate which of the two conditions is actually the more primitive. The length of the stump is regulated by the distance from the hinge of the wing at which the fracture line develops, but what governs this distance cannot be stated. Where the stump of the fore wing is considerably the larger—as in Calotermes and Cryptotermes—the atrophied anal field is within the stump, whereas it is partitioned in the hind wing, the fracture crossing the curved or oblique furrow which demarcates the anal field.

The fracture is due to an abscission forming quite late in nymphal life. If its ontogeny is not strictly analogous to the cell wastage leading to the falling of a leaf, it may be compared to what takes place with those plants in which the petioles are cut across at some distance away from the base so that, on the leaves separating, the base of the petiole is left attached to the stem. The development is not connected with any tracheal deviation, as has been suggested.

The anal furrow appears as a crease or fold after the final moult.

## V. THE RESPIRATORY SYSTEM.

Plates III to V, figs. 2–48.

As the wing tracheæ develop from tracheæ of the body, their genesis and growth and their diversified development may be better examined with some knowledge of the stem from which they spring and of tracheal growth and development occurring before they are produced. This involves a study of the respiratory system and its development. Naturally, the oldest tracheæ are those present in embryo; but, as these were not easily observed, the very young nymphs were examined.

It was my intention to base this chapter upon the tracheæ of the youngest forms of either Calotermes durbanensis or of Cryptotermes *sp.*; but in them the cardinal natal stem and its immediate development are too complicated to follow and to describe, although they can be understood with a knowledge of the simpler stem of the Metatermitidæ. Subsequently (Section V, f), a short comparison is furnished which deals with the points of difference found between the two forms. The present account relates to the simpler stem and some of its simpler post-embryonic developments, as observed in Termes natalensis, Odontotermes latericius, O. badius, Microtermes incertus, and Eutermes (trinervius group).

When these insects emerge from the egg they are provided with a respiratory system resembling a long, narrow crate, with ladder-like sides and bottom, with an open top and ends and possessing a few paired extensions. The whole is remarkably destitute of branchlets, and there are none of those arborescent tracheæ which develop later, and, to a great extent, shroud it.

The air enters through ten pairs of spiracles, two thoracic, and eight abdominal, and from the spiracles it passes into the system through short tracheal pipes.[1] Within the spaciousness of the head and the narrow confines of the neck and prothorax, the system is considerably modified; however, it is not independent of the rest, and the homologies of many of the parts there found with those of the thorax and abdomen can be determined, notwithstanding the very different appearance they present.

### Va. The Posterior or Body System.

Plate III, figs. 2–13.

Considered apart from the head, neck, and prothorax, the system posterior to the first pair of thoracic spiracles may be said to be composed of four longitudinals connected by two series of vertical and one series of transverse commissures. For convenience the longitudinals will be distinguished as the paired dorsal and paired spiracular trunks. There are no ventral longitudinal tracheæ. The upper pair, or dorsal longitudinal trunks, take an undulating course below the sides of the dorsum, extending from the prothorax to the caudal segments. The lower pair or spiracular trunks lie within the sides of the body against the spiracles, and are composed of a series of loops which link up the pipes in a somewhat indirect manner. Each spiracular trunk is connected with its corresponding dorsal by a regular series of palisade or vertical commissures, and the two spiracular trunks are directly connected by an equally regular series of ventral, transverse commissures. The extensions are: (a) the tracheæ of the second and third legs; (b) the ingrowing or visceral tracheæ, arising from each of the last six pairs of palisade commissures; (c) buds of arborescent tracheæ, set almost regularly along the dorsal trunks; and (d) paired buds and twigs upon the ventral commissures.

The examination of the arrangement in nymph after nymph, a small point here and another there, leads to the interpretation that the primitive abdominal region is built up by the sub-division or outbranching of the pipes. Each pipe seems to have given off three tracheæ: *a.*, an ascending vertical, *b.*, a descending transverse, and *c.*, a horizontal, fig. 2 (Pl. III). These three tracheæ appear to develop their courses as follows:

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[1] The term "pipe" is here used to distinguish the air passage leading directly from each spiracle.

Each ascending vertical, on reaching the roof of the body, dichotomises, its two branches take a horizontal direction, *a.a.*, fig. 3 (Pl. III), one extending backwards, the other forwards. Each meets and anastomoses with the corresponding branches of the vertical tracheæ of the next spiracles.[1] Thus is formed on either side of the body a palisade of arches, the bows forming the dorsal longitudinal trunk tracheæ. The caudal branches of each ascending trachea of the last abdominal spiracles grow as a cauda to each dorsal longitudinal trunk, fig. 4.

Each descending transverse trachea, on reaching the floor of the abdomen, crosses it, and thereby meets and anastomoses with the corresponding trachea of the opposite spiracle, fig. 5, and so a ventral commissure is formed.

Each horizontal trachea extends forward, *b.* of fig. 6, until it anastomoses with the descending trachea of the spiracle anterior to that from which itself arose. Thus are formed the spiracular longitudinal trunks, fig. 7. There being ten pairs of spiracles there are ten pairs of pipes, ten ventral commissures, ten pairs of vertical (or palisade) commissures, and nine sections to each spiracular trunk.

This simple segmental arrangement in the abdomen becomes more modified in the thorax.

The tracheæ of the second and third pairs of legs, fig. 9, are attached to the spiracular trunks where these traverse the meso- and metathorax. They are Y-shaped, and the stem of the Y has arisen by the coalescence of the two tracheæ forming the arms. Further evidence of this is found in the temporary separation of the two (*x.x.*) within the tibia.

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[1] "The term "spiracle" is here used to include the stoma, occluding apparatus and tracheal pipe. This is justified upon ontogenetic grounds, as it will be shown that the stoma, to which the term "spiracle" is legitimately applicable in the adult insect, is a transformation of the occluding apparatus, and in certain distended queens the "spiracle" is but a remnant of the pipe.

The six pairs of visceral tracheæ take an inward and then cephalic course, and as each pair traverses the whole of two sections the anterior pair enter the region of the metathorax, *x.x.*, fig. 10.

On the dorsal longitudinals, paired buds *x.x.x.x.*, etc., fig. 11, occur almost regularly upon each section or arch and later develop into arborescent tracheæ, fig. 12, which extend transversely under the dome of the dorsum, towards the median region.

Upon the first, third, and fifth to tenth commissures there are two buds, on the second there are four, and on the fourth there are none, fig. 13.

## Vb. The Cephalic and Prothoracic System.

### Plate III, figs. 14–19.

The stem within the head, neck, and prothorax lies before the first pair of spiracles, and these aerify it, figs. 18 and 19 (Pl. III). Its most conspicuous feature is a great U-shaped trachea which projects through the prothorax, neck, and occipital foramen, and lies close to the floor of the head, fig. 14. This is an anastomosis of the cephalic terminals of the two spiracular trunks, but may owe its origin to the linking up of the terminals by a transverse commissure. From the dorsal surface of each stem of the U just anterior to the spiracles and within the prothorax, arises a large dorsal trachea (marked *x.* in figs. 14 and 15). Each dorsal accompanies its corresponding stem of the U-shaped trachea through the neck and foramen, each then ascends into the dome of the head, and, extending forwards, terminates (*y.*, fig. 15) in the tip of an antenna. Each is again connected, or braced, within the head, to the U-shaped trachea by a vertical commissure (fig. 15, *z.z.*). These two upper tracheæ are the cephalic terminals of the dorsal longitudinal trunks.

The extensions of this part of the respiratory stem are:

(a) The tracheæ of the first pair of legs, fig. 16. The basal attachments of these are simple; they are linked together by a transverse commissure traversing the floor of the neck, the cervical commissure (*c. c.*, fig. 16).

(b) The paired tracheæ of the anterior lateral extensions of the prothorax (*a.a.*, fig. 17). These are somewhat insignificant and arise near the base of each of the upper main tracheæ (*x.x.*) between the spiracle and the point at which the dorsal longitudinal of the body (*b.b.*) is attached.

(c) The tracheæ of the vertex (*d.d.*, fig. 17) and of the genæ (*c.c.*). They arise in the order mentioned from each of the upper main tracheæ shortly after these enter the head.

(d) The paired complexi of the frons (*e.e.*, fig. 17), each complex being a bunch of three dichotomised tracheæ. A complex is attached to each of the upper tracheæ above the point of attachment of the vertical commissure (*z.z.*).

(e) The paired tracheæ of the lower mouth-parts and the paired tracheæ of the labrum, figs. 18 and 19. These emerge in the order mentioned from each stem of the U-shaped trachea. Each trachea of the lower mouth-parts subdivides into three stems. Of these, the innermost stem travels forwards and subdivides into three branches, one branch entering the glossa, another the paraglossa, and the third the labial palpus. The middle stem behaves likewise, its three terminals resting in the lacinia, the galea, and the maxillary palpus. The outermost stem enters the mandibles, extending to the apical tooth and giving off two side branches, one to the cutting and one to the molar region. Each trachea of the labrum travels upwards to the region of the clypeus, and there bears a complex or bunch of three tracheæ, and then enters the labrum, extending along the margin of this part to the apex. Fig. 18 has been prepared from a cleared preparation, and shows all the visible tracheæ as seen from below, the nearer tracheæ being shown in solid black and those travelling to the dorsal region lightly shaded. Fig. 19 shows a side view from below, and is also drawn from a cleared preparation of the head of a newly-hatched nymph; in this figure the tracheæ of the parts upon the further side of the head are omitted. It also illustrates the linking up of the cephalic with the body system.

### Vc. The Spiracles.

Plate V, figs. 22a–45b.

The spiracles or stigmata of an insect are defined as openings in the body-wall through which the air passes into the tracheæ. Such as are permanently open are regarded as the more primitive or generalised and those with lips as secondary or more specialised. In the case of both types, any occluding apparatus that may occur is said to be internal; e.g. a piece of mechanism intervening between spiracle and tracheal pipe. In all the species that I have examined such bivalvular types as have been met with have the valves partly external and partly internal, one folding slightly over the other to close the orifice. Moreover, when abdominal, such spiracles are but modifications of an occluding apparatus which formerly (in the nymphal stages) intervened between a fixed opening, or pore, and the pipe. For this reason it is proposed to refer to the apparatus from pore to trachea as the "spiracle," whatever condition it may be in; and the remarks, upon the structure, mechanism, and development which follow, relate to Termes natalensis *Haviland*, unless otherwise stated.

As the greater interest attaches to the abdominal series, the spiracles of the thorax have not been examined with particular attention. It may be said of them that they exhibit a simple bilabial form in the nymph and have no remarkable metamorphosis. In the adult the first pair is smaller and different from the second, the latter being shaped like a pair of buttocks. Both retain something of their labial form, figs. 38a, b, c (Pl. V). They are, however, valvular and closed and opened by special muscles. The tracheal pipes of which they are the mouths are united to them by a short tessellated rim and undergo changes in appearance as growth proceeds, changes which do not affect their tracheal character although transforming them into air-reservoirs. The anterior reservoirs assume a bottle-shape and the hinder become cordiform. Fig. 22A (Pl. V) is a sketch of the juvenile condition found in Microtermes incertus and its development is shown in figs. 22B to E. All the sketches are from individuals of the same species and all except E are drawn to the same scale, E being represented on a smaller scale. The tracheæ shown in part are: 1, the dorsal; 2, the spiracular of the prothorax and head; 3, the trachea of the first leg; 5, the passage to the second spiracle; and 4 is the ventral commissure which issues from the base of 5 to which it is attached on the visceral side of the air-sac. Figs. 22F, G, H represent the development of the pipes of the second spiracles in a less number of stages. The stage shown by 22F accompanies the development shown by figs. 22A, B, C; 22G accompanies 22D; and H accompanies E, but is drawn on a large scale. The tracheæ shown in part are: 1, the passage to the first spiracle; 1a, the passage to the third (or first abdominal) spiracle; 2, the palisade commissure to the dorsal-longitudinal; 3, the ventral commissure. This development applies equally well to that of T. natalensis.

Considered as a series, each pair of spiracles may be referred to by a number; thus the two thoracic pairs become I and II and the abdominal eight III to X. Briefly stated, III to X of the winged female of T. natalensis are bivalvular structures which are the final form of the post-embryonic type, III being more advanced than the rest. The bivalvular form of III of the female is only arrived at by III of the winged male; in this sex the remainder, IV to X, are arrested in a stage closely approaching that exhibited by the whole abdominal series in the nearly mature female nymph. The soldiers and workers display a slightly less advanced form, somewhere between the spiracle of the young and that of the nearly mature male nymph. In the case of the queen of T. natalensis and also the queens of Odontotermes *spp.*, there is a post-adult change in spiracles IV to X which may be described as a disruption of the organ, the valves being torn asunder. In mobile queens, those that have the free run of the hive, such as Eutermes (trinervius group) and Hodotermes viator and others, this disruption does not occur. It may also be mentioned here that in winged females of Hodotermes *spp.* the whole series III to X attain to an equal condition, fig. 35, and in the male, IV to X attain to a stage somewhat more advanced than that of the winged male of Termes natalensis. Compare figs. 36A, B, C with fig. 31A. The thumb-like process or bracket of the resister is a very pronounced development in Hodotermes.

For a considerable period of nymphal life, the spiracles of the abdomen are more or less unchanged. In the newly-hatched young, this organ (measuring approximately 0·08 mm.) looks like a little pitcher with a long neck and a round mouth. The mouth is the pore, the neck the atrium; and the ascidium, as it may be called, is the lever. Each spiracle lies in a dorsal position within the rolled-in edge of the tergite, and its long axis is parallel to that of the body, the pore facing backwards; and, except in the adult female (series IV to X), the caudo-lateral corner of the tergite forms a hood over it. Lying as it does, it has four aspects: a dorsal, a ventral, an internal or visceral, and an external. Upon the visceral side there is an outlet, formed by the separation there of the atrium from the ascidium; through this the air passes from the spiracle into a short membranous tube, and from this into the mouth of the pipe. Since the pipe is directed downwards and outwards it slants towards the spiracle and makes its union with it somewhat at a right angle. At the base of the atrium there is a vestige of a small plate. The spiracle and its connections, therefore, comprise the features shown in fig. 23A.

Taken separately, these may be described as follows:

(1) The pore or stigma; a circular opening surrounded by

a stiffened rim which is inserted into the cuticle of the body-wall.

(2) The atrium; an elongate and wrinkled cylindrical tube distended at the pore by a more or less regular tessellated framework of a hexagonal pattern; the approximation of the strands forming the heavier chitinisation of the rim of the pore, fig. 37 (Pl. V). At the end of the atrium, on the visceral side, is a small plate (2a) which is the "resister." The atrium seems to lead directly into the ascidium of the lever.

(3) The lever; this lies exterior to the trachea and has every appearance of being a simple membranous sac; but, as it is rigid, only its visceral side can be membranous.

(4) The epi-trachelos; a small membranous tube whose mouth surrounds the opening between atrium and lever and through which the air passes into the trachelos. It is the mouth of the epi-trachelos which is closed by the bending of the lever towards and across the resister, fig. 23c.

(5) The trachelos is the hexagonally tessellated and bulbous foot of the tracheal pipe.

The developments which first take place are more or less concurrent. The lever gradually loses its vesicular form and so changes to a plate which is slightly concave on the visceral side and convex on the external side. Figs. 25a, b, c represent the lever in vertical section and show what appears to take place. The resister of the atrium develops a deep hiatus, the hiatus arising from the ingrowing of the lower median region, which now protrudes into the lumen, figs. 26a and b. The region of the atrium adjacent to and anterior to the resister becomes prominent and chitinised, forming a "chin-plate" (*ch.*, fig. 30). The epi-trachelos is absorbed into the trachelos which extends and reaches to the opening between atrium and lever. These changes produce the spiracle of the second stage with its quoit-like rim, figs. 24a and b.

The opening and closing of the lumen is brought about by a band of muscle. This has three fixed insertions, the first is to the chin-plate (*ch.*, figs. 28a and 30) slightly anterior to the resister; from here it passes diagonally to the tip of the lever; from the lever it extends outwards slightly and is fixed to the tergite just within the cephalo-lateral corner, on the line where the chitinisation begins to be less dense. The strap of muscle from chin-plate to lever contracts and draws the lever towards and somewhat across the foot of the resister. The resister and lever are linked by a flexible band which acts as a fulcrum but not as a spring, the lumen being opened by the strap of muscle extending from the lever to the tergite.

The transitional conditions between the second and the third stage differ mainly from the second in the noticeable decrease in the length of the atrium. The shortening of the atrium is a gradual process due to the throwing off of the rim of the pore at each ecdysis. Fig. 30 shows a spiracle about to enter upon the third stage, and a new rim (*nr.*) is seen in the course of formation behind the pore (*pr.*). Another feature is the marked differentiation of the chin-plate.

The spiracles IV to X of the male may be taken as representing the third stage. This form is shown, fig. 31A, from the visceral aspect, and the attitude of the lever when open and shut is indicated below the fragment of the trachelos. In the illustration it will be noticed that the resister has become strongly compressed and that the chin-plate has acquired an auricular form; it is almost transparent, but possesses a chitinised margin. The lever, it will be observed, has suffered no reduction.

Fig. 31B illustrates diagrammatically the external and 31C the dorsal aspect of the organ, the atrium being separated from the closing apparatus. These two figures are designed to show what happens in the case of spiracle III of the male and spiracles III to X of the female, the whole of the atrium being thrown off excepting the chin-plate and resister. This leaves the interior surface of the chin-plate exposed on the body surface and also the anterior edge of the lever, so that these parts now form the valvular pore or stigma. The resister is further reduced and forms one edge of the mouth of the spiracle. Fig. 32 represents spiracle III and figs. 33 and 34 show the form of spiracles IV to X of the female and illustrate the reduction of the lever.

In fig. 32 the resister (*R.*) is reduced and to it is attached the visceral edge of the trachelos (*m. tr.*) and it still performs its original function of closing against the much modified but strongly developed lever (*L.*), behind which the trachea is seen. The chin-plate (*C.*) is fixed in the cuticle of the body-wall. The occluding muscle (*oc. m.*) still extends from it to the lever and the extensor muscle (*ex. m.*) to the margin of the tergite.

The spiracles of the queen, being more of the nature of tracheal development, are dealt with in the next section, Vd. The condition seems due to the great distension of the conjunctiva, but this does not explain it wholly, as the tearing away does not occur in other queens, which enlarge considerably. The elongate depressions that result have many pits in them, like ear-holes, and into these many tracheæ open freely.

## Vd. Tracheal Growth and Modifications.

Considered apart from the cardinal stem of the respiratory system, the growth and development of tracheæ is tree-like. A trachea grows indeterminately or with a marked tendency to dichotomise. It sends out branches which behave similarly. As the branches increase in length and number, the stem enlarges as does the trunk of a tree. In their ramifications the tracheal course is, on the whole, like that of a root in the soil; with most, however, the field of growth is controlled and a particular region is invaded, but the detail of movement appears ungoverned. This is illustrated by the arborescent branches of the dorsal-longitudinal trachea in fig. 12 (Pl. III), and in the branching of the leg-tracheæ, fig. 39 (Pl. V).

One of the outstanding developments occurs in the case of the pipes of the abdominal spiracles of the female. These are originally simple tubes subdivided into three, as described in Section Va. As the nymph develops, a great number of individual tracheæ arise, figs. 50A, B, C (Pl. VI); from each pipe these grow as in figs. 41 and 42 (Pl. V), and the majority of them travel to the paired ovarian cords which lie within the pluræ. To these they attach themselves like the tentacles of an octopus and form great brushes, figs. 43A, B (Pl. V). This development follows a considerable distension which first takes place at the junction of the three primary subdivisions of the pipe as illustrated in fig. 40 (Pl. V). This phase is succeeded by those shown in figs. 41, 42, and the final nymphal form is that illustrated in figs. 43A, B; A showing an external and B an internal view. In B are to be seen the two muscles behind the spiracles, and below the ovarian cord a part of the peristaltic ribbon is also shown. In these figures it is seen that tracheæ now extend down the pipe and enter a short, broad dilatation. The transformation of the spiracles has already been explained, and the disruption in the case of IV to X of the queen mentioned. Fig. 44 shows a side view of one of this series of spiracles, and it will be noticed that all the tracheæ now open into the cup-like mouth of the pipes. With disruption the valves are shredded to fragments, and the trachelos or mouth of the pipe is now the spiracle, the nature of which is illustrated in figs. 45A and B.

Tracheæ may be modified by the volume of the air-route. In the following section, wherein an attempt is made to homologise different parts of the system, use is made of this feature to explain the disguised bases of a number of palisade commissures. For example, in the nascent stage whilst the pipes of spiracles V to X divide into three principal stems, one of these stems, instead of appearing to be a palisade commissure, seems to be the visceral, with the palisade as a vertical growth therefrom. This change in the arrangement (see fig. 10, Pl. III), is due to the enlargement of the direct route to the part demanding the greater supply of air.

### Ve. The Homologies of the Main Stem.

In figs. 18 and 19 (Pl. III) and 20A and 20B (Pl. IV), an attempt is made to show the natural arrangement of the nascent stage of the respiratory system. Of the four, fig. 20B is an external aspect of the arrangement upon the left side of the body, and forms the basis of the diagrams used to illustrate the homologies. Fig. 20A (Pl. IV), is more or less diagrammatic (see Explanation of Plates).

It is not difficult to resolve the system of the trunk into a regular scheme by alterations of a minor nature; the abdominal spiracular loops are straightened to accord with their appearance in the winged imago, wherein they seem to stretch taut from spiracle to spiracle; the series of palisade and ventral commissures are also altered to accord with one another, the two palisades of the thorax being somewhat lengthened to agree more in height with the rest. Thus, the system of the head, neck, and prothorax can be first resolved into the scheme given in fig. 46 (Pl. V), in which it is shown connected with the trunk system. This rearrangement of the tracheæ enables us to see (1) that the basal part of the cephalic dorsal (or antennal) trachea is a palisade commissure that has been thrown down and inflated; (2) that the anterior vertical commissure (connecting the dorsal trachea with the stem of the great U-shaped trachea) may be regarded as a palisade commissure, and that the stem of the U is the continuation of the spiracular trunk. The first inference to be drawn is that the arch of the U is a modified ventral commissure. If this is the case, then there are two pairs of palisade commissures, and, counting the cervical as one, two ventral commissures which are not associated with spiracles. On this it may be assumed that two spiracles have been lost to the system. It is obvious that the meso- and metathoracic leg-tracheæ, fig. 9 (Pl. III), owe their Y-shaped form to the anastomosis of two tracheæ. In view of the separation of the tracheæ in the tibia of the front leg, fig. 16 (Pl. III), it is reasonable to assume that the base of this was also composed of two tracheæ. The commissure of the neck connects the tracheæ of the first pair of legs some distance below their attachment to the spiracular trunk; but it is not unreasonable to suppose that it was originally attached to the spiracular trunk as are other ventral commissures, and that its bases have fused into the leg-tracheæ. If, then, the tracheæ of the mouth-parts are directed ventrally, they correspond with the leg-tracheæ. These alterations appear in the diagram fig. 47 (Pl. V). This diagram illustrates that (*a*) the trachea penetrating the anterior lateral and dorsal extension of the prothorax corresponds with the visceral trachea of spiracles V to X, and is not a wing trachea, as might be readily supposed; (*b*) the trachea of the antenna is the homologue of caudal trachea. The tracheæ of the gena and vertex are probably analogous to the arborescent tracheæ which develop from the buds of the dorsal longitudinal trunk. The difference is that there are two instead of one, but it frequently happens that two arborescents arise from a section of the trunk, and it is not altogether rare for one section to be budless and one or the other of those adjoining to possess two buds.

The complexi of the frons and of the clypeus appear to be without homologues.

Although the visceral tracheæ are regularly confined to the palisades V to X, occasionally, and as a later development, an analogous branch may arise from palisade IV; this is included in fig. 47 (Pl. V).

From fig. 18 (Pl. III) it will be seen that the tracheal twigs which enter the glossæ, paraglossæ, and labial-palpi have their homologies in the twigs entering the laciniæ, galeæ, and maxillary-palpi. Further, the tracheæ of the mandibles are homologous to those of the labial mouth-parts insomuch that each extends to the apical tooth, and sends one branch to the cutting region and another to the molar region of each mandible. In this connection it may be mentioned that the mandible of the nymph of a Eutermes (trinervius group) strikingly exhibits three well-defined regions; the apical tooth being the homologue of each palpus, the cutting region of the galea and paraglossa, and the molar region of the lacinia and glossa. (See inset on Pl. IV.)

## Vf. The Calotermite Stem.

Plate IV, figs. 21A, B, C.

The respiratory system possessed by the young of Calotermes and Cryptotermes on leaving the egg is more ample and more complex than is the Metatermite form. Moreover, it becomes more complex as growth proceeds. Apart from this, various structural features—especially the sculpture of the head and the compression of the thorax—alter the courses of the tracheæ, produce unusual post-embryonic developments, and make its detailed examination more difficult.

For the purpose of this section it will be sufficient to compare briefly the system of Cryptotermes with that of Termes natalensis. The first difference to be noted is the presence of an extra pair of longitudinal tracheæ which lie along the floor of abdomen and thorax, fig. 21A (Pl. IV). These may be said to be composed of a series of loops linking up the ventral commissure, and extend from the commissure of the first to that of the tenth pair of spiracles, continuing beyond the last in a tail-like form into the ventral caudal region, and so resembling the tails of the dorsal longitudinal trunks. This extra pair of tracheæ is also exhibited by Calotermes durbanensis, Hodotermes *spp.*, and by Rhinotermes putorius.

In slightly more mature nymphs of Cryptotermes there is a striking X-shaped trachea across the floor of the prothorax (fig. 21A). This arises out of the brief anastomosis of the median point of the cervical with that of the ventral commissure of the first spiracles. The two tracheæ are approximated at birth and joined by a short isthmus; they gradually fuse, and later are stretched taut so as to form a regular X. A similar trachea has been observed in Calotermes, but it appears to originate differently, and has not been satisfactorily studied.

Except for the extra pair of longitudinal trunks and the **X**-trachea, the characters of the stem of the thorax and abdomen are agreeable with those of the Metatermite form; but the cephalic arrangement is quite different.

The simple **U**-shaped trachea formed by the extensions of the spiracular trunks into the head is wanting, whilst the continuations of the dorsal longitudinal trunks are more amply developed.

The spiracular trunks projecting into the head cavity each have a tree-like form, and their stems are linked together by a transverse commissure placed well back so as to give an arrangement resembling the letter H. In the region of the labium each trunk subdivides into three principal stems which supply the mouth-parts, fig. 21A (Pl. IV). Upon the whole, their arrangement is like that seen in T. natalensis, but the paired tracheæ of the labrum arrive within the clypeus by a more indirect route. They first bend outwards more or less at right angles to the parent stems, travel behind the eyes, and then upwards into the dome, bending sharply inwards to the clypeus; here they turn forward at a right angle and pursue a remarkably straight course into the labrum. They may be said to traverse the inside of the head capsule from their point of origin to where they turn out of the clypeus. As in the Metatermite form, so in this the spiracular tracheæ are connected with the main dorsal tracheæ by upright commissures, but these are both very incurved and **C**-shaped. As development proceeds they become approximated and then fuse at the point of contact to form an **ƆC**-shaped combination.

In more mature nymphs of Cryptotermes, Calotermes, Hodotermes, and Rhinotermes there is a decided **Y**-shaped trachea between the two dorsal tracheæ (those which have their terminations in the antennæ), the arms of the **Y** being attached at the same points as are the vertical **C**-shaped tracheæ just described, fig. 21B. This middle trachea undoubtedly originates in Cryptotermes from two tracheæ, each an inner basal branch of the dorsal tracheæ. These issue from the stem just where the dorsals enter the head cavity. They have the appearance of having grown together in the embryo, and after anastomosing, one becomes arrested, the other extends forwards and crosses and anastomoses with an out-curved, transverse commissure which connects the two dorsals. This problematic development results in the arrangement found at birth, as illustrated by fig. 21c (Pl. IV). The change of appearance that results later, fig. 21B, is no doubt due to the strain of structural developments, and these draw the middle trachea into a position which is approximately in the longitudinal axis of the head.

## VI. THE TRACHEÆ OF THE WING-SAC, THEIR GENESIS AND GROWTH.

### VIa. The Tracheæ.

The tracheæ of the wing-sac are outgrowths from those sections of the spiracular trunks lying within the meso- and metathorax, and, with two minor exceptions, they have been found to originate between the bases of the Y-shaped tracheæ of the second and third pair of legs, fig. 48 (Pl. V). The outstanding exception to this rule occurs in T. natalensis. In this insect the base of the post-costal is frequently beyond that of the anterior arm of the leg-trachea. In Hodotermes viator it was once found similarly situated, but in this species the post-costal is less frequently independent of the radial than it is in T. natalensis. The rule holds good for the local representatives of the following genera that have been examined: Hodotermes, Calotermes, Cryptotermes, Rhinotermes, Microtermes, Eutermes, Hamitermes, Cubitermes, Procubitermes, Promirotermes, and Microcerotermes. The tracheæ have either two or three connections. In the representatives of the genera Calotermes, Cryptotermes, Eutermes, Hamitermes, Cubitermes, Procubitermes, Promirotermes, and Microcerotermes there are regularly three. To these connections with the cardinal stem it is proposed to apply the terms radial root, medial root, and cubital root. The anterior is called the radial because the scape continues uninterruptedly into the wing-sac and precedes the rib to which the name radius has been applied (see Section III). In Calotermes and Cryptotermes the post-costal and sub-costal are regularly attached to the radial trachea, the one to the root, the other to the scape. In those species presenting no post-costal the sub-costal is regularly attached to the radial scape. The middle root is called the medial because it is that of the trachea which precedes the media. The posterior is described as the cubital because the scape enters the wing-sac uninterruptedly and precedes the cubitus; to its base is attached any rudimentary anal that may be present. In H. viator there are usually two and occasionally three, in Termes natalensis there are occasionally two, more often three, basal connections. When there are two they are the radial and the cubital, and the radial trachea then carries the post-costal and sub-costal, as in the other species, whilst the cubital trachea is in a duplicated condition, the inner stem preceding a typical cubitus, the outer a pseudo-media. When there are three connections, the condition is due to the occasional independence of the post-costal trachea, fig. 78 (Pl. VII), an independence which manifests itself quite erratically in T. natalensis as regards any of the four wings of a given insect. At the base of the cubital trachea of T. natalensis there is an anal trachea; this does not grow into the wing-sac, however, but turns inwards and enters the thoracic cavity, figs. 182, 186 and 187 (Pl. XI).

In Microtermes there are usually two basal connections and occasionally three. When two are present they are as in T. natalensis, the cubital being always duplicated (the post-costal appears to be often wanting, but when present is attached to the radial). When three are present the extra one is the medial; thus a wing-sac of the species of this genus may present an independent medial in company with a pseudo-medial and a cubital, fig. 200 (Pl. XI).

In Rhinotermes putorius there are three roots; these I regard as the post-costal, the radial, and the cubital. The post-costal is a shortened trachea whose position is analogous to one of the two independent phases of this trachea in T. natalensis. The radial is a simple trachea with a few weak outer branches. The cubital is a duplicated trachea as in Termes, Hodotermes, Odontotermes, Microtermes, and abnormally in Calotermes. Occasionally the cubital root carries three tracheæ and the more anterior of these may be regarded as the medial trachea (see figs. 165, 166 (Pl. X), and discussion, Section IXd).

### VIb. The Genesis of the Wing-sac Tracheæ.

Plate VI, figs. 49–59.

In any adult termite, the two pairs of equally diaphanous wings extend, when folded, to about the same point. In other words, the hind wings are shorter to a fixed degree than the fore wings. This condition is achieved by the earlier appearance of the fore wings; and it is frequently possible to detect two phases of tracheal growth in the organs of one insect, the tracheæ of the fore wings being slightly older they are usually a little more advanced in growth than those of the hind. Much that is said in this and the next subsection rests upon this circumstance, as, naturally, it has not been possible to examine the continuous development of the wing tracheæ in one insect.

The lateral extension of the meso- and metathorax—the beginning of wing-growth—takes place when the insects are very young, about 1·5 to 2 mm. in length. In Cryptotermes, in particular, the genesis of the tracheæ seems to occur before there is any obvious lateral extension. The sections of the spiracular trunk first bulge outwards, and, having assumed this position, buds arise, fig. 51 (Pl. VI), and soon develop into tubercles. In Cryptotermes[1] the buds become tubercles which are almost regularly clavate, fig. 52, but in other species they are conical, fig. 53. It is during the development of the buds into the tubercle form that the extensions of the meso- and metathorax become noticeable. With the first marked extension a scape grows from each tubercle, and very frequently on one side of its apex, fig. 54. These three scapes (or stalks) extend into the wing-sac as simple tracheæ and are the radial, medial, and cubital tracheæ; the differentiation between the basal tubercle and its scape soon disappearing. In Termes, Odontotermes, and Microtermes (and presumably Hodotermes) the cubital tubercle early assumes a bifid form and two stalks grow from it, fig. 55.

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[1] The account from here onwards of growth of tracheæ refers in particular to this generalised species, and to Calotermes durbanensis; any point at which a more specialised species differs is the subject of special remark.

In Calotermes and Cryptotermes it has been observed that before the differentiation between scape and tubercle takes place, a secondary tubercle forms near the base of the radial, fig. 56, and from this develops the post-costal trachea. At this stage four simple tracheæ occur in the wing-sac. Soon after the post-costal has developed a little, the vermiform bud of the sub-costal appears upon the radial stem, fig. 57, and this grows into a stalk, so providing the wing-sac with five tracheæ. Still later, the anal issues from the root of the cubital, fig. 58, so that there are six simple tracheæ, fig. 59. Not until all have made some growth does any one produce branches.

## VIc. The Growth and Development of the Wing-Sac Tracheæ.

From the foregoing account it will be gathered that the tracheæ of the wing-sac arise in an orderly sequence. Those first appearing are the ones which normally develop the strongest; that is to say, where there are three roots, the strongest tracheæ are the radial, the medial, and the cubital, and, where there are two roots, the strongest are the radial and the duplicated cubital.

For Calotermes and Cryptotermes, the preliminary development may be summarised as follows:

(*a*) The bulging outward of the spiracular (or cardinal) trunk as in figs. 49, 55 (Pl. VI).

(*b*) Bud growth (radial, medial, and cubital), fig. 51.

(*c*) Development of buds into tubercles, fig. 52.

(*d*) Growth of the scape of the radial, medial, and cubital tracheæ, fig. 54.

(*e*) Appearance of the bud of the post-costal, fig. 56.

(*f*) Development of post-costal.

(*g*) Appearance of sub-costal, fig. 57.

(*h*) Appearance of anal, fig. 58.

(*i*) The elevation of the extended bow of the cardinal from the horizontal to the perpendicular, fig. 60.

The foregoing sequence of events applies to other species having three basal attachments except that with some *e*, *f*, and *h* do not occur. It also applies to those species of which the wing tracheæ have only two basal connections except that either no medial or no post-costal nor anal develops.

The elevation of the bow of the cardinal, or the lifting of the latter to the plane of the meso- and metanota, is necessitated by the forming of a "shoulder" to the wing-sac. It is accentuated by the downward "drag" of the leg-tracheæ upon it (see fig. 60, Pl. VI).

Ordinarily, where there are three basal connections, that of the medial is closer to that of the cubital than it is to that of the radial, in young nymphs (fig. 52). An opposite state of affairs occurs subsequently and the base of the medial is far removed from that of the cubital, sometimes to a very great extent, figs. 203, 205 (Pl. XI). The change of position is due to a considerable intercalary growth of the cardinal, which occurs between the roots of these two tracheæ. Because of this secondary growth, the scape of the cubital lengthens in proportion to the degree to which its attachment is carried further and further from the mouth of the wing-sac.

A feature of much interest is the behaviour of the trachea that enters the wing-sac behind the radial. This may be the true medial or the pseudo-medial (outer cubital), but its origin makes no difference to the regular behaviour seen in the wings of more mature nymphs. In all cases, on entering the wing-sac it approaches the radial. In the hind wing it is briefly applied to the radial, bending back again to a median position; in the fore it does not reach to the radial, but recedes and becomes briefly applied to the cubital, from which it bends off again to a median position.

This trait may be taken as evidence that, where there are two basal connections, the base of the medial trachea has migrated to the base of the cubital; but against this is the evidence furnished by the frequent duplication of tracheæ in Calotermes and the frequent occurrence of a true independent medial, in the presence of a duplicated cubital, in Microtermes incertus. Moreover, in Hodotermes, Termes, Odontotermes, and Microtermes both stems of the cubital develop along similar lines; a similarity of development which is most marked in Hodotermes and Termes.

The subsequent development of the wing tracheæ comprises the following:

(*j*) The production of main branches—or offsets.[1]

(*k*) The growth, from stems and offsets, of innumerable tracheal fibrils.

In the last nymphal instar the wing-sacs are pervaded with tracheæ—especially those of the more generalised species—and it is by no means uncommon for the principals and their sub-divisions to extend and travel—usually in the direction of the base of the wing-sac—along the edge of the marginal thickening, figs. 78, 94 (Pl. VII); these extensions may also bend back into the body of the wing-sac, fig. 142 (Pl. IX).

Apart from the normal, many cases of apparently abnormal development have been noticed; that is to say, a principal trachea is often duplicated.

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[1] It is convenient to apply the term "offset" to the regular series of main branches of the cubitus exhibited by all species, and also to the series of outer branches of the radius possessed by Hodotermes, Calotermes, and Cryptotermes.

The duplication of principals is very frequent in Calotermes, where all have been found in this condition except the radial. It is also common enough in Cryptotermes.

### VId. Reduction of Tracheæ.

In the final wings of Calotermes durbanensis numerous abnormalities of the venation are directly traceable to pre-existing extra principal tracheæ. As evidence of this is also to be found in the wings of other species, one is justified in concluding that the predecessor of the termite wing was a tracheated organ into which many more principal tracheæ penetrated than is ordinarily regarded as the full complement, and perhaps the production of these exceptional tracheæ may be regarded as reminiscent of an ancient ancestor.

In an earlier section it has been shown that the development of the tracheæ of the wing-sac occurs in an orderly sequence. Making allowance for reduction in area, it is equally true that both the gradual reduction of some principal tracheæ and the loss of others takes place in an orderly sequence; this reduction may be described as a gradual retirement along the line of advance.

Of the principal tracheæ, the sub-costal and the anal are the latest to develop, and should, on the foregoing premises, be the first to disappear. However, as a rule, it is the post-costal that is earliest lost, then the anal, and, lastly, the sub-costal; this slight derangement of the sequence being no doubt due to the narrowing of the basal area of the wing.

The post-costal is quite extensive and many-branched in Hodotermes karrooensis and H. transvaalensis. In H. viator it is weaker and less branched. In Calotermes and Cryptotermes it is, comparatively speaking, weakly developed and but rarely branched, and is more atrophied in the hind wing than the fore wing. It is a shortened and simple trachea in Rhinotermes putorius; reduced and inconstant in Termes natalensis; and, in Microtermes *spp.*, it appears as a fine, short trachea, or fails altogether to develop. The sub-costal trachea is often branched in Hodotermes; it is more often simple in Calotermes and Cryptotermes. In Termes natalensis and Microtermes it is shortened and reduced, fig. 176 (Pl. XI), and in Rhinotermes it is missing. In most of the Metatermitidæ examined it is either absent or very much reduced.

The radial is strongly branched upon both sides in Hodotermes. The inner branches or sectors are wanting in Calotermes, Cryptotermes, and Rhinotermes. In all the other species except T. natalensis, both inner and outer branches are missing or very much reduced. Thus, in the case of Rhinotermes there are very reduced outer branches with no inner. In Termes natalensis there is a regular series of outer branches, but ribs do not arise from them in the final wing, and in this and certain Odontotermes there is a tendency—possibly due to reversion—for the radial to produce relatively strong inner branches; in some wing-sacs of one and the same insect these are present, in others absent.

When present the anal trachea is much reduced in all the species studied, and in T. natalensis it enters the thoracic cavity and not the wing-sac.

A further feature which may be mentioned in this connection is the tendency for the tracheation of the wing-sac, as a whole, to become reduced by the failure of the principals to produce that multitude of fibril-like branches so characteristic of the wing-sacs of the more generalised species, and practically absent from those of the more specialised.

## VII. THE VENATION AND UNFOLDING OF THE FINAL WING.

Plate VI, figs. 61–69.

Hitherto, in discussing the nymphal wing, a fairly flat organ has been under reference, and this, when cleared in glycerine jelly, reveals the air-laden tracheæ stretched out upon a fairly level plane. This condition obtains until the insect has progressed well along the last nymphal stadium. It is then succeeded by a phase in which the tracheæ are found sinuate and later coiled and overlying one another, fig. 61 (Pl. VI). This is due to the growth of the final wing and the lengthening of the tracheæ with it. The cuticle encasing it cannot give way along its margin, but both the upper and lower surfaces bulge outwards, the growing wing accommodates itself to its narrow confines by a series of longitudinal folds and transverse creases, and so becomes packed up very tightly.

From quite early stages pale bands are to be seen in the organ. As the largest of these cause faint ridges to form on the dorsal surface of a wing-sac but leave no other trace on the moulted cuticle, they must represent a certain differentiation of tissue. Their structure has not been studied, but they no doubt consist of modified cells which form about the tracheæ and cause thickenings between the upper and lower cuticles. The principal tracheæ have not been noticed dissociated from them, but this is not the case with some of the branch tracheæ. Consequently, certain pale thickenings are found in which there are no tracheæ. As development proceeds certain tracheæ tend to move out of the thickenings. After such a movement a further thickening may or may not form about the latest course of the trachea and hence one and the same trachea may give rise to two thickenings. Two concrete illustrations may be taken from the wings of Calotermes durbanensis.

The first is the frequent presence, in the final wing, of a bicornute branch near the base of the mediæ, lying between it and the radius, figs. 112 (Pl. VIII), 127 (Pl. IX). This rib is derived from a similarly shaped, pale thickening that is occasionally to be seen in a wing-sac, and it depends upon the stage in which the tracheation of the wing-sac happens to be whether this is or is not associated with a trachea. When it is so, the trachea is furcate, with the tips of its branches turned backwards, fig. 62A (Pl. VI); when it is not, the furcate trachea is present but differently disposed, fig. 62B (Pl. VI).

The second illustration furnished by the wing of this species is to be found in the field of the cubitus. This, in the final wing, frequently displays more or less interrupted, erratic, or independent ridges between the cubitus offsets, some being ill-defined, others plainly marked. These ridges are due to the pendulum-like swinging of the offsets of the cubital and to the formation of stronger or weaker thickenings about them, in their earlier positions. In short, a thickening once formed tends to persist, and so gives rise either to a ridge or a rib. Figs. 63A, B are diagrams designed to illustrate this point. Fig. 63A represents the first position of two cubital offsets. In fig. 63B these are seen to have moved forward, leaving the thickening behind. The deserted thickenings become ridges in the final wings, and those occupied by the tracheæ become ribs.

As the final wing develops it forms into longitudinal rolls, and into these is gathered all the tissue. The rolls soon become contorted and vermiform; they appear coiled up and apparently inextricably mixed, fig. 64. In this condition the wing is unsheathed.

However, complicated as the arrangement looks, it is not difficult to see that each roll is the counterpart of a rib that will form in the final wing. In other words, the tissue has centralised along the courses of the thickenings. Inasmuch as the tracheæ also grow one would expect to find them to be the cores of those thickenings that formed latest about them. This is so in part, but not wholly, and the condition seems to be due to the tracheæ not attaining to the same length as do the rolls, and, therefore, not following all the plications.

Well before the final ecdysis, the imaginal wing becomes surrounded by a layer of air which separates it from its sheath.

After the moult, the adult is white and soft-bodied. The wings remain tightly packed, except for the expansion of their basal region. Pigmentation, which synchronises with chitinisation, takes place very slowly and not until after the wings have fully expanded. First the head, then the body and legs, and last the wings become coloured and hardened; the whole process taking place in complete darkness. The pigmentation of the head and of the sclerites appears to begin at a central point and then to spread outwards; that of the wings begins at the roots, and has the appearance of flowing along the ribs and out from them into their branches, whether such branches were preceded by actual tracheal connections or have arisen from the fusion of thickenings forming about approximated or applied tracheæ. For this reason a cross-rib is usually more strongly attached to the more chitinised of the two principals it connects although, ontogenetically, it may be a branch of the weaker. The unfolding and hardening of the wing is a peculiarly slow process. After the last moult, the wings of C. durbanensis unfold in the course of several hours—probably three or four—but nearly a full week elapses before the body is fully chitinised and the wings hardened. Throughout the greater part of this period there is a distinct lumen in the post-costa, sub-costa, radius, media, and cubitus and the main offsets of these ribs, whilst a lumen representing the anal trachea lies within the anal field, fig. 68 (Pl. VI). Except the basal branch of the post-costal, *x*., fig. 68, there is no such lumen in the marginal nor in the cross-ribs, minor branches, and ridges. The lumen is a capillary air-tube from which the air slowly disappears, often giving the effect of a broken column of mercury in the tube of a thermometer. When the wings are first unfolded traces of the tracheæ can be made out here and there, more especially at the bases of the wing, and then the spiral is drawn out, fig. 69. In Termes natalensis and allied forms, the expansion of the wing and the complete hardening of the adult seems to proceed much more slowly, and there is some reason to believe that the better part of a month elapses before the adult insect is perfectly developed.

The unfolding and spreading of the wing takes place from the stump outwards, as seen in the nine diagrams, figs. 65A to K, prepared from wings of T. natalensis. During this period the insect walks about holding out its wings in the attitude depicted by fig. 66. The process may well be likened to the billowing out of a crumpled and wet cloth by driving a blast of air below it, compare figs. 67A, B, C, D, which represent wings of T. natalensis in four degrees of unfolding. In this insect the tracheæ may be found, practically intact, in the wing stumps; but there are no air-passages through the ribs, fig. 67D. The radius, pseudo-media, and cubitus appear, however, perforated by a minute capillary, which is probably ill-defined because filled with a fluid. What seems to happen to the tracheæ is that they are stretched until the spiral is unwound, and are then absorbed; this conclusion is based upon the occasional presence of frayed-out tracheæ in the more apical part that has just unfolded; such were present in the wing shown as fig. 67D. It is very obvious that the minor tracheæ are absorbed, and there is some reason to believe that this takes place before the final ecdysis.

## VIII. THE VARIATION IN THE VENATION.

Some reasons have already been stated which will account in part for the variation in the venation and for the extreme variableness of the reticulation.

Final wings differ so much in detail that it is impossible to put aside as quite alike any two, even of one insect. It may, however, be said that the more specialised the species, the more is the venation of one wing agreeable to that of its companion, and, the more generalised, the greater the irregularities. This is largely because the more generalised species have more reticulate wings.

In the preceding section the statement is made that thickenings form about the tracheæ. To this it may be added that the ribs of the final wing are transformed thickenings. The point that the marginal arises from a cuticular thickening which does not form about a trachea has been sufficiently emphasised.

Indeed, for all the rest of the venation it may be laid down as an axiom that where there is no preceding trachea there is no succeeding rib or even ridge. To this it may be added that when the growth of a trachea is weak or when a trachea is undeveloped the succeeding rib is similarly affected. Upon the other hand, it is equally true that thickenings do not necessarily form about all minor tracheæ, and consequently every such trachea does not invariably give rise to a rib in the final hardened wing.

Variations in the venation are mainly to be traced to the variation of the tracheation. This is well illustrated in Termes natalensis. For this species it may be stated that the radial may have from 0 to 5 strong inner branches (sectors), the pseudo-medial may be deeply furcate and many-branched or practically simple, the cubital may be over-developed or under-developed. If, of the three, the pseudo-medial is more or less simple, then either the radial possesses sectors or the cubital is over-developed. Usually, if the pseudo-medial is well-developed the radial has no sectors, and the cubital presents either a medium or an under-developed condition. When the radial possesses sectors and the pseudo-medial is well-branched, the cubital is under-developed.

The only other influencing factor seems to me to be the hardening of the wings, to which may be traced breaks and dislocations and actual obliterations. It has to be borne in mind that when finally expanded the termite wing is soft, and days, perhaps weeks, must elapse before it is hardened and rigid. The upper and lower surfaces, never far apart, are drawn closer together, and the process of their union tends to smooth out any rib or part thereof that may be weakly formed. So much is this the case that a branch of the cubitus may lose its basal connection and appear as an independent, from the margin. Obliteration is very marked in T. natalensis. In this species the freshly-expanded wing exhibits, in detail, a reticulation that the pre-existing tracheation has given rise to, but as the wings harden this completely, or almost completely, disappears; the degree differs apparently in different races. The same factor also obliterates that portion of the marginal which extends along the inner edge.

It may be said literally that the final wing mirrors the main tracheæ of the wing-sac with remarkable precision, and, with minor exceptions, it is a fact that the ribs represent the tracheal arrangement. Fused ribs arise from the amalgamation of thickenings. It has been shown that anastomosis may occur within the body of Cryptotermes between tracheæ, which touch one another, but nothing of this sort has been found in the wing-sac. Tracheæ may apply themselves closely to one another, or they may cross one another in the wing-sac, but they do not anastomose.

Independent ribs are to be sought for between the offsets of the cubitus. In the Metatermitidæ they are usually offsets that have lost their basal connections. In Cryptotermes they succeed thickenings forming about the ingrowing tips of cubital offsets, figs. 142 (Pl. IX), 146, 149 and 152 (Pl. X).

The following details regarding the variation of the venation as a matter apart from the presence of extra ribs and other extraordinary conditions, are given in a condensed form. The subject is one that can be considerably elaborated, but to do so would serve no useful purpose. In all instances the results given are based on the examination of the wings of the insects of one nest in one season.

### Hodotermes viator (*Latreille*).

The post-costa is simple, as a rule, but it may exhibit one or two minute offsets to the costa, more particularly in the fore wing.

The sub-costa may also have one or two outer branches; in rare instances there are more than two, and then well-developed.

The radius has both outer and inner branches. The outer branches, or offsets, ordinarily connect with the costa; but one or two, near the apex, tend to extend towards the wing-tip, taking a more or less parallel course with and between radius and costa. The number of offsets is variable, 3 to 6, and any one may be simple or subdivided. The inner branches, or sectors, are variously developed, the more basal being frequently atrophied; when few in number all may reach the inner margin of the wing; when many, most are atrophied. The sectors may be simple or much subdivided; the subdivisions may anastomose among themselves or with the pseudo-media. The sectors present in a wing range in number from 3 to 6, of which 2 to 5 may reach the wing-margin.

The pseudo-media is, exceptionally, simple, fig. 84A (Pl. VII), usually it is deeply furcate; when furcate its two main branches may be simple or subdivided. Its subdivisions may extend to the margin at 1 to 4 points. In some cases the subdivisions are anastomosed to the radius sectors and cubitus, fig. 84C, and occasionally are so absorbed that the pseudo-media may appear as not extending to the wing margin.

The cubitus exhibits a variable number of offsets, 8 to 12, which are either simple, furcate, or more subdivided.

The anal of the hind wing is extensive when compared with the trachea it succeeds, and almost invariably fuses with the basal offsets of the cubitus, figs. 70B (Pl. VI), and 84B, C, D (Pl. VII).

The wings of other local representatives of the genus have similar diversities. Larger wings differ only in that the post-costa displays stronger and more numerous branches, fig. 70A (Pl. VI), and the sub-costa is more frequently branched.

Analysis of ten wings of H. viator:

Post-costa: Simple, 7; with one branch, 2; with two branches, 1.

Sub-costa: Simple, 2; with one branch, 6; with two branches, 2.

Radius: With three offsets, 2; with four, 4; with five, 3; with six, 1. With three sectors, 3; with four, 1; with five, 5; with six, 1.

### Calotermes durbanensis *Hav.*

The wing venation of this species is much more variable than that of any other species examined. That the venation also exhibits a wider range of extraordinary conditions has no bearing on the matter of the variability of the venation. A monograph would be required to deal with this subject, its extent being limited only by the number of wings available. Although in many of the wings illustrated on Pls. VIII, IX, the venation is abnormal, they serve very well to illustrate the features here discussed.

The post-costa, independent on the fore wing only, is regularly simple, but it merges into the costa anywhere between one-quarter and one-sixth the length of the lamina.

The sub-costa is generally simple, but occasionally it may exhibit one outer branch. It unites with the costa at any point from one-half to three-quarters the length of the lamina.

The radius possesses 4 to 8 offsets to the costa. These are mostly simple and straight, but they may be variously subdivided or they may be imperfect, or they may anastomose with one another. In 29 fore wings, counting subdivided offsets as one, the average and common number was 7; in 28 hind wings the average and common number was 5; the range was, however, the same for both fore and hind wings. The irregularity of the subdivision of the offsets is illustrated as follows: Of 47 wings, 24 possessed simple offsets, 13 had one furcate offset, 9 had two such offsets, 1 had three and 1 four; the remaining 8 had one offset with two branchlets.

The media is usually simple; it may, however, be furcate or well-branched. In the case of 62 wings (fore and hind) 21 had a simple media, 26 a media with a minor apical prong, and 15 a media more or less well branched.

The cubitus exhibits a variable number of offsets; these are generally simple, while some may be forked or even more subdivided. The subdivided offsets vary from 0 to 5. Counting subdivided offsets as one, in 31 fore wings the number of offsets varied from 8 to 13, the average being 10 and the common number 12. Similarly, in 28 hind wings, the range and average being the same, the commonest numbers were 10 and 11.

The cross-ribs between media and radius vary widely in number, form, and arrangement. The reticulation between media and cubitus may be represented by a simple ridge, by a feather-stitch, a festoon, or a lace-like pattern. The ridges between the offsets of the cubitus are rarely if ever the same in any two wings.

### Cryptotermes *sp.*

These are interesting little wings exhibiting an erratic arrangement in the outer apical quarter, between cubitus and radius.

The post-costa (fore wing only) has always been found simple and varying only in length.

The sub-costa was simple in all wings noticed, and 52 were specially examined for the purpose.

The radius of the fore wing has 6 to 9, and of the hind wing 4 to 7 oblique offsets to the costa; these are normally simple, only one forked branch being found in 52 wings. The radius of the hind wing may possess as many offsets as that of the fore wing, but generally it has from 1 to 3 less. The common number for the fore wing was found to be 8 and for the hind 6. The following table represents the arrangement for 8 individual insects:

| Wing. | Left. | Right. | Left. | Right. | Left. | Right. | Left. | Right. |
|---|---|---|---|---|---|---|---|---|
| Fore . . | 7 | 7 | 8 | 7 | 7 | 8 | 8 | 8 |
| Hind . . | 5 | 7 | 7 | 7 | 6 | 5 | 6 | 5 |
| Fore . . | 7 | 7 | 8 | 8 | 7 | 9 | 8 | 9 |
| Hind . . | 7 | 6 | 5 | 6 | 6 | 6 | 6 | 7 |

An analysis of 20 fore and 25 hind wings gave:

| | Fore wings. | Hind wings. |
|---|---|---|
| Radius with four offsets | 0 | 1 |
| ,, ,, five ,, | 0 | 6 |
| ,, ,, six ,, | 1 | 12 |
| ,, ,, seven ,, | 6 | 6 |
| ,, ,, eight ,, | 9 | 0 |
| ,, ,, nine ,, | 4 | 0 |

Not infrequently (20 per cent.) the media possesses a sector that extends in a straight or sinuous course to the apex of the wing; when this is present the cubitus is restricted; when absent, the cubitus is more extended.

## Termes natalensis *Hav.*

The simple radius may exhibit well-defined inner branches or sectors which curve shortly to the apex of the wing. When present the number varies from 1 to 4.

The pseudo-media may be practically simple, that is, with a furcate tip in the apex of the wing; more frequently it possesses 1 to 3 strong inner branches which are simple or erratically subdivided. In 18 wings before me, 6 have the pseudo-media with one, 6 two, and 6 three such branches. In 31 wings where the pseudo-media was found more or less branched, the first branch originated before half the length in 8, at half in 18, and beyond half in 5 cases. In one of these wings two branches originated before half the length. The inner margin of this wing is supported by the branches and the subdivisions of the pseudo-media and the offsets of the cubitus. In order to ascertain whether there was any degree of consistency in the number of points at which the margin was so supported, 12 wings were examined with the following result:

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| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Pseudomedia | 2 | 5 | 6 | 6 | 6 | 6 | 6 | 7 | 8 | 10 | 11 | 13 |
| Cubitus . | 29 | 17 | 18 | 20 | 21 | 22 | 27 | 18 | 22 | 25 | 18 | 15 |
| Totals . | 31 | 22 | 24 | 26 | 27 | 28 | 33 | 25 | 30 | 35 | 29 | 28 |

### Microcerotermes *sp.*

In the particular species under reference the wings may be said to have specialised towards a more or less fixed venation. The diversities although small are still frequent. The radius is always simple. The media may be simple or furcate or further subdivided. In 24 wings it supported the margin at four points in 1, at three in 7, at two in 12, and at one in 4. The offsets of the cubitus are, on the whole, simple; one of the series may, however, be furcate. The number of offsets ranges from 8 to 12, the average and common number being 10. None of the wings of this Microcerotermes showed any abnormality (24 examined); but, from those of a smaller species,[1] the media was often absent.

### Microtermes *sp.*

In this species, of which 10 wings were examined, the media was usually furcate. In 5 the prongs were short, in the others more profound. When this latter condition occurs each prong may be more or less subdivided, so that the media may support the margin at 2, 3, 4, or 6 points. Occasionally the diversity of the venation is added to by the branches of the media crossing the cubitus. The offsets of the cubitus are on the whole simple; in 5 of the 10 wings, 1 furcate offset was found. In the 5, where all were simple, the number present ranged from 10 to 13.

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[1] Probably M. zuluensis *Holmg.*

## IX. SPECIAL WING STUDIES.

### IXa. HODOTERMES *spp.*

Pl. VII, figs. 78–84D.

The wings of various Hodotermes all possess a very similar scheme of venation, such differences as do occur being chiefly the degree of coarseness in which the ribs are displayed. At one extreme stands H. karrooensis, fig. 70A (Pl. VI), at the other H. viator, figs. 84A to D (Pl. VII). The ribs, in the former species, are not only more gross than those in the latter, but the branching of some, particularly the post-costa and sub-costa, is more ample and the "reticulation" more decided.

The ribs *Pst. C.*, *Sc.*, *R.*, *Ps. M.*, *Cu.* and *A.* are preceded by tracheæ. The costa may not be so strongly developed as the radius, especially towards the apex of the wing, and its continuation around the inner margin is much obliterated. It extends along the outer edge of the wing-stump, but is attenuated or thinned out at the root of the wing.

The post-costa forms the anterior articulation of the wing and extends as a strongly chitinised ridge through the wing-stump into the lamina. It is connected with the costa by a short curved branch or strut, which occurs outside the line of fracture in the fore wing, and inside of it in the hind, and is preceded by a branch of the post-costal trachea, *x.*, fig. 78 (Pl. VII).

The pseudo-media unites in the hind wing with the radius well outside the line of fracture, fig. 70B (Pl. VI). In only one wing has a deviation from this rule been found, and in this, fig. 71 (Pl. VI), its union with the radius took place at the line of fracture. In the fore wing, the pseudo-media enters the wing-stump, there its base merges into the bases of the radius and cubitus, fig. 70A (Pl. VI).

The anal of the hind wing may be described as a prolongation of the somewhat pyriform anal lobe of the stump; it projects much further into the lamina than one would expect from the atrophied condition of its pre-existing trachea.

It will be noticed, figs. 70A and 75 (Pl. VI), that the sub-costa is as independent of the radius as is the cubitus, in both wings. Apart from variations the wings of Hodotermes do not present many abnormalities, and several hundreds have been examined for the few illustrations here given. In the case of H. viator: (a) two wings were found in which the sub-costa was duplicated, figs. 72A and 72B; (b) one wing in which it was deeply furcate, fig. 73, a condition that may have arisen from a duplication of the pre-existing tracheæ; (*c*) one wing with the post-costa deeply furcate, fig. 74; (*d*) the sub-costa appeared in a strongly-branched condition, fig. 77, unusual for this species. In the case of H. transvaalensis: (a) in one wing there was no pseudo-media, fig. 75 (Pl. VI); (b) the pseudo-media occurred in a duplicated condition, fig. 76.

My studies of the tracheæ of the wing-sac have been practically restricted to H. viator, and then to the organs of almost mature nymphs. The majority of specimens examined conformed with that illustrated, fig. 78 (Pl. VII). This shows: (a) the post-costal with an independent basal connection (see also fig. 82 and compare with figs. 80, 81, 83, Pl. VII); (b) a duplicated cubital; (c) the anal attached to the stem of the cubital near the fork of the two cubitals. The anal is generally in this position, but may often have a more independent position, fig. 83, and may be decidedly subdivided as in this particular instance.

The abnormalities noticed were: (a) in one wing-sac the inner cubital was much reduced, fig. 79 (Pl. VII), whilst the outer, or pseudo-medial, was strongly developed; (b) in three wing-sacs three tracheæ were attached to the cubital stem (as seen also in Rhinotermes), in one of these the outer of the three was considerably atrophied, but in the others, fig. 80, it extended practically to the apex of the wing-sac; (c) in one wing-sac, fig. 81, the post-costal was duplicated; (d) in one wing-sac an extra trachea was found entering the wing-sac and closely applied to the radial along a part of the length of the latter, fig. 82; unfortunately the basal connections of the tracheæ were broken, and the figure represents all that could be made out.

## IXb. CALOTERMES DURBANENSIS *Haviland*.[1]

Plates VIII–IX, figs. 38–134.

Altogether between 400 and 500 wings of this insect and quite 100 wing-sacs in various stages of development have been examined. The wing examinations show that, apart from those almost individual peculiarities previously grouped as variations (Section VIII) about sixteen wings in each hundred exhibit a more or less abnormal venation. It may be gathered that a marked variation is characteristic of the species, and not of individual colonies, from the fact that such obtains in five colonies from distinct centres, although the bulk of the total cited was made up of 227 wings from one colony and 165 from one another.

In the tracheation of the wing-sac and in the venation of the wing this Calotermes differs fundamentally from Hodotermes. In the wing-sac the medial is always present, and normally the cubital is not duplicated. In the wings, the two most striking differences lie (i) in the absence of sector branches from the radius of Calotermes; (ii) in the seeming absence of the post-costa from the hind wing, a rib that is strongly defined in the hind wing of Hodotermes (compare fig. 86 with figs. 84B, C, D, Pl. VII). Other differences are: (a) the position of the median rib; this, as the true media in Calotermes, extends to the apex of the wing and is sub-parallel to both radius and cubitus; (b) the presence of a series of cross-ribs connecting the radius and media; these do not occur, as between pseudo-media and radius, in Hodotermes; (c) the noticeable fusing of the media with the cubitus of the fore wing, fig. 85 (Pl. VII), outside the line of fracture.

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[1] For the determination of this termite see Appendix.

In the stump of the fore wing the costa and post-costa seem to arise from a common stem. The costa is, however, joined by a branch from the post-costa, see fig. 68 (Pl. VI), and the costa, in a somewhat diminished form, extends around the front margin of the stump. In the hind wing the costa suffers a diminution at relatively the same point so that it enters the wing-stump as a reduced rib, and here, as in Hodotermes, the post-costa is one of the chief ridges of the wing-stump. Of all the hind wings examined, the post-costa fused with the costa shortly after entering the lamina, fig. 86 (Pl. VII), with two exceptions. In these it was almost independent of the costa in the laminæ, fig. 87 (Pl. VII). In only one fore wing was the post-costa found fused to the costa, and then so that the two formed a "double-barrelled" rib.

The variations of the venation can only be understood and the abnormalities explained by a study of the development and behaviour of the pre-existing tracheæ. Much of this has already been alluded to at length in other sections. Attention may here be drawn to the development of the tracheal system as illustrated by the series of camera lucida sketches rendered as figs. 88 to 94 (Pl. VII). The following points will be noticed: (a) the constant presence of the post-costal trachea in the hind wing-sac; (b) the building up of the main system, fig. 93; (c) the secondary development of minor tracheæ accompanied by the lengthening of the main series, fig. 94; and (d) the "pot-bound" effect caused by the marginal thickening.

Notice may also be taken of the varied development of the anal or anals. Commonly there is a single simple anal present, figs. 92 and 97; not infrequently the single anal is furcate, figs. 94, 95 (Pl. VII); rarely it is three-pronged, fig. 99A (Pl. VII). Quite often there are two anals, and both may be simple, figs. 93, 98A, or one may be simple and another pronged, fig. 96. Inhabiting an atrophied part, the anal is, in whatever form, atrophied; that, when displaced, it is capable of considerable development is illustrated subsequently.

In comparatively young nymphs one finds abnormal tracheal departures, and there is no evidence to show that the complicated arrangements, to be discussed, are due to physical injuries. The following series of abnormal schemes are selected to indicate the range of departures from normal development, and are arranged from the more simple to the more complicated.

Fig. 95 (Pl. VII) represents an abnormal medial which has developed two strong branches, both of which accompany their parent stem to the apex of the wing, but cross one another in their progress there. The crossing of tracheæ is very frequent in the case of branches from principals, and principals themselves often cross. In fig. 96 (Pl. VII) the medial is seen crossing the cubital and invading its field. An event of this sort usually leads to the part atrophy of one of the tracheæ, in this case the media, and the over-development of the other. It results in the formation of large elongate cells in the final wing and those illustrated in figs. 118, 120 (Pl. VIII), 125, 127, 128, 130 (Pl. IX) seem to owe their condition to this factor. These wings are much like others, figs. 113 (Pl. VIII), 119 (Pl. VIII), but here the median cells may have arisen from the coming together of tracheæ (as in Cryptotermes) and not from crossing.

Fig. 97 (Pl. VII) illustrates a fairly simple case of a duplicated trachea, the medial, and is selected to show extra features; i.e. the crossing of the two and the part atrophy of one. Fig. 98A (Pl. VII) illustrates another case of a duplicated media. It differs from the former insomuch that the duplication seems a secondary condition, the outer medial appearing as a growth from the inner, fig. 98B (Pl. VII). In this case the two extended through the median field and reached to the wing apex. Fig. 99A shows a simple duplication of the cubital trachea, and fig. 99B how the extra trachea originates opposite the seat of the anal. In this case the two tracheæ maintained a cubital character; that is, both had offsets to the inner margin of the wing-sac, as is the habit of the pseudo-media and cubitus with Hodotermes and other species to be mentioned later.

Fig. 100 (Pl. VII) is a rare example of a duplicated post-costal in the presence of a duplicated cubital, and it will be noticed that the inner post-costal has crossed the radial proximally to the base of the sub-costal.

Fig. 101A (Pl. VII) is a remarkable scheme that owes its origin, in the first place no doubt, to the entrance of the cubital into the wing-sac anterior to the medial. In intruding itself into the middle region thus the cubital carried its duplicated anal into a false position and the two anal tracheæ have grown enormously. As a consequence of this there is only one normal trachea, the post-costal, present. An anal intrudes between it and the radius; the radius is reduced to a simple trachea and the sub-costal has failed to develop. The second anal intrudes between the radial and medial and upon the medial falls the aerifying of the outer apical margin. It accomplishes this by developing radial characters, producing a series of three strong outer offsets. The cubital, it will be noticed, crosses back again over the medial, fulfils its normal functions, and at the same time produces two strong branches to aerate the region normally supplied by the medial. Fig. 101B illustrates the connection of the anal with the cubital.

Fig. 102A illustrates the most extraordinary case met with. In this wing-sac three principals are duplicated—the sub-costal, the medial, and the cubital. The outstanding feature of the scheme is the remarkable S course taken by the inner of the two cubitals, but the grave disturbances are due to the excessive development of the two sub-costals. This leads to a somewhat similar condition to that seen in the wing-sac illustrated by fig. 101A. Here, instead of the anals, it is the sub-costals that bring about the atrophy of the radial, and here, as before, the supplying of the loss falls on the medial, the outer of the two medials assuming a radial form and function.

From the foregoing examples it will be seen that all the principal tracheæ, except the radial, are liable to duplication; all except the cubital, to a certain amount of reduction. In only one case was anything approaching a duplication of the radial found. This is illustrated by figs. 103A and B. The chief interest attaching to this example lies in its uniqueness.

Figs. 104 to 134 (Plates VIII–IX) illustrate a number of wings selected from insects of one nest series which show a wide range of diversities and abnormalities. For convenience the word "wing" will be used instead of "figure," and it will be understood that whilst the drawings essay to picture the actual arrangement as far as possible, they do not show the marked difference that actually exists between the rigid and the flexible ribs.

Wings 104, 105, 108, 109, 112, 114 are all normal. Wings 107, 110, 111 are normal, but illustrate the occasional and more or less simple furcation of the media.

Wing 106, otherwise normal, possesses a remarkably well-branched media.

Wing 115 illustrates a unique case in which the media is drawn close to the radius.

Wing 116, whilst apparently but a more exaggerated illustration of an amply branched media, as in wing 106, more probably owes its condition to a duplicated medial.

The condition of wing 117 can be safely traced to a duplicated medial trachea. This wing is remarkable for the sharp and deep incurving of the tips of both media, the pre-existing tracheæ in this case, probably turning back as decidedly as tracheæ do in the wing-sacs of Cryptotermes, a feature that is further illustrated by wing 126.

Wing 121 is a hind wing in which the media is attached to the cubitus instead of to the radius, and this unusual state of affairs is accompanied by a short extra rib which occupies the place where the media would normally stand. Such a rib may arise from any one of several tracheal conditions. It might be due (a) to an extra but atrophied medial; (b) to a branch of the radial, as in fig. 103A (Pl. VII); (c) to a duplication of either the post-costal or the sub-costal, as in figs. 100 and 102A.

Wing 122: this abnormality can readily be traced to a duplicated medial, as in fig. 98A, the two tracheæ becoming so closely applied to each other at half the wing-length that but one rib formed. Wing 123 equally owes its abnormal condition to a duplicated medial, both medials being atrophied and the tips of both touching the radial. The venation here illustrates the extra development of the cubital to make good the atrophy of the medial. Wing 124 owes its condition to a duplicated cubital, as in fig. 99A.

Wing 125 possesses a remarkable venation which does not give any very direct clue to the pre-existing tracheal tangle. It seems to me, however, to be due, in the first place, to a duplicated cubital, and, in the second place, to the crossing of the medial trachea by the outer cubital, so that the latter ran in between the medial and radial.

Wing 128 serves to illustrate the result following the crossing of principal tracheæ. Here it would seem that the medial was in duplicate, and the two stems crossed, somewhat as they do in fig. 97 (Pl. VII), the lower being briefly applied to the cubital. Wing 129 is one which conforms to the generic character for Cryptotermes, the media "joining the radius at about half the length of the wing." This is a case of the tip of a weak medial becoming applied to the radial.

Wing 131 suggests a duplicated medial in company with a duplicated cubital, the outer cubital being approximated to the medials. Wing 133 exhibits a duplication of the medial with the two tracheæ more or less atrophied and with the tip of each applied to the radial, the base of one associating itself with the radial and of the other with the cubital.

Wing 134 is a further illustration of a duplicated medial.

### IXc. CRYPTOTERMES *sp.*

Plates IX and X, figs. 135A–154.

Except that in ninety-nine of every hundred wings of this species the media is found united to the radius at or about half the length of the wing, the structure of the wing-stumps, figs. 135A and 135B (Pl. IX), and the relationships of the principal ribs are similar to those of Calotermes. That the generic character is not constant may be gathered from figs. 148 and 150 (Pl. X); it is true both the wings illustrated have an extra principal rib, but a normal wing has been found in which the media extended to the apex. Many wings are to be found in which the media possesses a strong branch or sector to the apex, such as those illustrated by figs. 143, 146 (Pl. X). This is seemingly the case in fig. 149, but here the condition appears due to the intrusion of an extra principal trachea into the wing-sac.

Cryptotermes wings differ strikingly from those of Hodotermes and Calotermes in the complete absence of reticulation. In many wings there are no ridges whatever; in others, again, there are curiously curved and erratically arranged ribs or cross-ribs exterior to the cubitus in the apical quarter, and these sometimes occur between the media and radius as in fig. 143. Where the media has no branch, the cubitus tends to invade its field, figs. 144, 147. "Independent" ribs are not uncommon; and they may appear actually independent as in fig. 152 or can be seen to be incurvings of the cubitus offsets as in figs. 146, 149.

Abnormalities due to the presence of extra principal tracheæ in the wing-sacs are to be met with, but not so frequently as in Calotermes. Such as have been found are traceable to a duplication of either the medial or the cubital trachea. Figs. 148, 149, 151 illustrate wings which seem to owe the unusual arrangement of the ribs to a duplicated cubital, whereas fig. 150 represents a duplication of the medial. In neither Hodotermes nor Calotermes was a hind wing found in which the pseudo-media or media did not attach itself more or less conspicuously to the radius; but one hind wing of Cryptotermes, fig. 152, shows the media attached to the cubitus.

The development of the tracheæ of the wing-sac has been dealt with elsewhere, and is similar to that of Calotermes, except there is no secondary development of many fibril-like tracheæ. A few do develop and are the predecessors of the small cross-ribs already alluded to. The main tracheæ and their offsets do, however, lengthen considerably. Often the terminals of the radial, medial, and cubital travel for a considerable distance around the margin, and a remarkable extension of the cubital tip is shown in fig. 142 (Pl. IX). This wing-sac also illustrates the almost regular habit of the cubital offsets to dichotomise and for the branches to intermingle or turn back into the wing-sac.

The basal arrangement of the tracheæ is similar to that of Calotermes. This is shown, as seen in a preparation, by fig. 140 (Pl. IX).

In both fore and hind wing-sacs the post-costal and anal are present. In the younger nymphs the tracheæ first penetrate and develop in the wing-sac in more or less straight and parallel courses. In fig. 136 (Pl. IX) only the radial, medial, and cubital have developed. Two later stages are represented in figs. 137 and 138; both illustrate the late development of the anal. The radial and cubital branch about the same time; and, after this takes place, the tip of the medial inclines towards that of the radial, fig. 138; as the wing-sac grows, they extend, closely applied to each other, to and around its apex. When applied to the radial the medial is usually the more tenuous of the two. It may run quite evenly with it, fig. 139A; or entwine it, fig. 139B; or leave it abruptly, fig. 139C; or produce a straight or sinuous offset, figs. 139D and E; or an atrophied offset, fig. 139F. Sometimes the medial or its main offset bears one or several very fine branches, fig. 139G.

Further, after meeting the radial the growth of the medial may stop, or vice versâ, the radial may grow no further. In this event the medial assumes the function of the radial, simulating it by sending a series of branches to the outer margin. Abnormal schemes of tracheation were not met with in the long series of wing-sacs studied, other than the peculiar development of a trachea from the radial root shown in fig. 153 (Pl. X). The most unusual scheme was that reproduced by fig. 154.

## IXd. RHINOTERMES PUTORIUS *Sjostedt.*

Plate X, figs. 155–166.

The following notes are based upon too few wings and wing-sacs to be at all conclusive. As far as the observations go, they are, however, sufficiently interesting and important to include.

The Rhinotermes wing has much in common with the Metatermite type, more especially the more generalised as represented by Termes and Odontotermes. The principal differences lie in the absence of any trace of the sub-costa and in the greater area of the stump of the fore wing. As in the Metatermite wing the outer margin is supported by a pair of equally rigid, closely set, simple, and parallel ribs, and the remainder of the wing field by two principal flexible ribs. As compared with the wings of Hodotermes, Calotermes, Cryptotermes, the outer field is remarkably reduced. The two outer ribs are the costa and radius, and although no auxiliaries lie between them in the lamina, and the radius sends no branches to the costa, the two are connected by a number of struts, each forming a narrow isthmus and all arranged like the rungs of a ladder, figs. 155, 156 (Pl. X). The two remaining ribs I recognise as the pseudo-media and cubitus. In the fore wing these two fuse at the line of fracture, but within the wing-stump they are separated by a conspicuous fusiform space, fig. 157 (Pl. X). In the hind wing, the pseudo-media is attached to the radius just outside the line of fracture, and in this wing there is a marginal anal so atrophied as to be almost negligible, fig. 158.

The pseudo-media is more amply branched than in Hodotermes; and, as the radius has no inner (or sector) branches, it extends to the apex of the wing. Because it partakes of the nature of the cubitus it is well branched and the offsets of these two ribs support the inner wing-margin.

In figs. 157, 158 it will be noticed that in the wing-stump the costa is divided; the lower branch is the post-costa.

The foregoing interpretation is based upon an examination of the tracheæ of the wing-sac. Some young nymphs, with eight or nine months of development still before them, exhibited peculiar and somewhat erratic buds of wing tracheæ, and figs. 160 to 163 illustrate the conditions found in one of them. Fig. 160 shows the post-costa, radial, and furcate cubital; also a vestigial sub-costal on the radial. Fig. 161, although belonging to the mesonotum, is very different; here a similar post-costal is set much nearer a radial that wants the vestigial sub-costal, and against the stem of the furcate cubital springs a strong bud which may be considered as that of the medial. Fig. 162 is a condition analogous to that shown in fig. 161; the post-costal is, however, well removed from the radial and a medial springs from the stock of the cubital. Fig. 163 represents a fourth and very different condition; here the post-costal is as in the other wing-sacs, whilst, apparently, the radial and medial both spring from the stock of the cubital. Just what the subsequent development might be it is impossible to say, but in twenty-three out of twenty-four wing-sacs from six older nymphs, wanting a month or two for maturity, the condition of the tracheæ was as shown in fig. 164, except that in some the furcation of the cubital was much deeper-seated, so that the stock appeared to be double-barrelled. The tracheæ in the wing-sacs of these older nymphs probably had not reached their full development. It is to be noticed that the post-costal is fairly short and that the radial has similar branches to the radial of Hodotermes, Calotermes, and Cryptotermes; these branches need not, however, be regarded as the predecessors of the struts connecting the radius and costa in the final wing.

The one wing-sac that was unusual presented an extra trachea, fig. 165 (Pl. X), which may be regarded as the medial. An examination of the basal connections showed that this extra trachea arose from the cubital stem, fig. 166, a condition that might well be expected from the juvenile conditions already described.

I have found no final wing with an extra rib, but, curiously enough, the reproduction of a photograph of the wings of this species (fig. 5, Pl. VI, Holmgren's 'Termitenstudien,' II) shows such an extra very clearly.

One feature of the Rhinotermes wing which the tracheæ, as studied, do not throw any light upon, is the marked extent to which it is ridged. This is so much the case that some ribs are not readily differentiated from the ridges. However, those between the offsets of the cubitus probably arise as they do in Calotermes, and the numerous oblique ridges between pseudo-media and radius may arise from tracheal branchlets of the former that had not developed in the wing-sacs studied.

### IXe. Psammotermes allocerus *Silv.*

Plate X, figs. 167–173.

In Rhinotermes it has been shown that the medial trachea and therefore the media is normally wanting; there is some evidence to show that it may be occasionally present. This is also the case in Psammotermes, and later it will be shown that in Termes natalensis an extended examination of wing-sacs and wings has failed to show any trace of a medial. Upon the other hand, the medial (and media) is regularly present with Calotermes and Cryptotermes, and although it tends towards decadency in the latter there is ample evidence of what may be described as an effort to re-establish itself as one of the principals. The conclusion one comes to is that in certain generalised termites the medial has become suppressed by the regular and strong development of a duplicated cubital. In Calotermes and Cryptotermes it has been seen that any deviation of the medial from its field or any atrophy that occurs is made good by the cubital. In short, the cubital seems ever ready to assume the chief aerating route of the wing-sac.

The following remarks upon the wings of Psammotermes are introduced only to illustrate the aggressiveness of the cubital. They are based upon the examination of twenty laminæ and have little other interest, as no wing-sacs of the nymphs of this species have been available for study. It is thought, however, that the tracheation is analogous to that of Rhinotermes except that the cubital is not regularly duplicated.

The outer field of the wing—as apart from the stump—is supported by two simple parallel chitinised ribs; these are the costa and radius. There is no trace of an intervening auxiliary or of connecting supports such as are found in Rhinotermes and Termes. Both costa and radius are, whilst rigid, quite slender, and the latter tapers off before the former. The wings examined fall into two groups, those in which a median rib is present, and those in which there is no trace of such. This rib I take to be the media because of its simplicity. When present in the fore wing, fig. 167 (Pl. X), it is fused to the cubitus, and, when present in the hind wing, to the radius, fig. 168. Of the twenty wings examined, such a media was present in seven; of these, two were fore wings and the rest hind wings. In the remainder the cubitus was highly developed, the degree varying as between figs. 169 to 173. In the hind wing there is present a very inconspicuous anal. It is possible that in some of the wings the cubital trachea was duplicated, but this is pure speculation.

### IXf. TERMES NATALENSIS *Haviland*.

### Plate XI, figs. 174–179.

As between the wings of T. natalensis (with its races and such local allies as T. bellicosus, T. swaziæ, and T. waterbergi) and those of Rhinotermes putorius there is a general likeness of structure, particularly as regards the nature and arrangement of the two principal ribs, pseudo-media and cubitus. Especially is this the case within the laminæ. Here, however, there are a number of differences, some more important than others. The laminæ agree insomuch that the outer margin is supported by a pair of close-set parallel ribs of equal strength and rigidity, the costa and radius. They also agree in that the membrane derives its main support from a pseudo-media and cubitus. The principal point of difference is that, inset between the bases of the two outer ribs, there is a short auxiliary, the rudiment of a sub-costa. Other differences that may be cited are: (a) the absence of an anal from the hind wing; (b) of struts between radius and costa (occasionally one such strut is to be found in the wings of T. swaziæ); (c) the obliterated condition of the "reticulation"; (d) the frequent presence of inner branches (sectors) to the radius. The general features of the Termes wing are illustrated in figs. 174, 175 (Pl. XI); but in these no attempt has been made to indicate the obliterated reticulation to which reference has been made, and both wings exhibit sectors to the radius.

Considerably over 100 wings of one nest series, together with a number of minor lots, were searched without avail for abnormalities of venation, and this is remarkable insomuch that the tracheation of the wing-sac is so extensive and in some particular features curiously variable. The full development of the tracheæ is traced in fig. 176 (Pl. XI) and parts of the scheme are drawn upon a larger scale in figs. 177 and 178. As in Hodotermes and Rhinotermes this tracheal display originates in the main from two roots or basal connections, the radial and cubital. Figs. 179 and 180 are sketches showing the genesis of wing tracheæ, 179 of the meso- and 180 of the metathorax. Here the normal condition appears reversed, a greater development having taken place on the cardinal of the metathorax. That this is unusual may be seen from fig. 181, wherein not only is the mesothoracic wing-sac the larger but the post-costal is present, whereas it has not yet put in an appearance in the metathoracic sac. In this particular instance the post-costal is in the position that is normal for Hodotermes, Calotermes, and Cryptotermes. The second development is that of a sub-costal, and later the anal may appear. The only principal trachea that is ever absent is the last mentioned, as in figs. 183 and 185. It may be present in an atrophied condition, fig. 184, but is generally well-developed, figs. 182, 187; as a rule it arises from the cubital, but has been found occupying an independent position on the cardinal as shown in fig. 187. In all cases, when present, the anal trachea is directed away from the wing-sac into the thoracic cavity. The basal attachment of the post-costal is most erratic. It may spring from the radial, figs. 184, 185; it may be independent (as in Rhinotermes), fig. 182, but more often it arises from the stock of an arborescent bunch of tracheæ anterior to the union of the cephalic arm of the leg-trachea with the cardinal, figs. 183, 186, 187. The radial usually stands independent upon the cardinal, but has twice been found close to, fig. 185, or arising from, fig. 183, the stock of the cubital. In but one nymph has anything approaching the development of a medial trachea been observed, fig. 187. In any one nymph of T. natalensis four differing conditions may be found as regards the basal connections of the tracheæ of the four wing-sacs.

With reference to the post-costal trachea it may be added that it is readily observed lying within the large outer shoulder-like ridge of the wing-stump of the adult, should the insect be fresh and not too long fledged.

### IXg. MICROTERMES INCERTUS (*Hav.*).

Plate XI, figs. 188–200.

The wings of this insect have the same structure as those of Termes natalensis, etc., but display less regularity. The main point of difference is that there is no inner branch to the radius in ninety-eight out of every hundred wings. Compare fig. 190 with others. Occasionally, the radius and costa are linked together by small struts, reminding one of those common to the Rhinotermes wing, but each is obviously an isthmus arising during chitinisation, figs. 188, 189, 193. The irregularity that is most noticeable is due to the rare presence of a true media, figs. 191, 192 (Pl. XI), and to the occasional union of this with the radius, figs. 192, 193. However, considering the frequency with which a medial trachea is present in wing-sacs, it is remarkable that more evidence of it is not to be found in final wings. It is possible, however, that the thickening forming about it coalesces with that forming about the pseudo-medial, and any branches it may produce appear in the final wing as branches of the pseudo-media.

From an examination of a considerable number of nymphs in various stages of growth, it is possible to say that ordinarily the tracheæ of the wing-sac arise from two buds, the radial and the cubital, of which the latter is the first to develop; compare figs. 195, 196 with fig. 197. In a later stage the three principals are found as in fig. 198. Still later, developments comprise, ordinarily, the branching of the cubital and the appearance of a sub-costal. Extraordinarily, a post-costal or an anal, or both, may appear, fig. 199, and either of these two tracheæ may lie extended into the wing-sac or may bend back into the thoracic cavity.

Quite frequently the wing-sac is penetrated by a principal trachea, extra to the normal quota; this is the medial, fig. 200. In all cases except one, in which such a medial was found, the cubital was duplicated. In the one exception the cubital was single, but the medial was duplicated.

Concerning the wings reproduced it may be said that figs. 188, 189 represent companion fore and hind wings, both of which may be considered as normal, but the condition of the hind wing, fig. 189, gives rise to the suspicion that the venation is due to a true media as well as a pseudo-media and cubitus. Fig. 190 represents a normal wing; the only one noticed in which the radius possessed a true inner branch or sector. Fig. 191 is a wing in which the media is undoubtedly fully developed, and in the two wings, figs. 192, 193, I think the rib which unites with the radius arises from a true medial trachea. Fig. 194 represents a quite abnormal condition due to the pseudo-medial trachea applying itself in part to the radial.

## IVh. MISCELLANEOUS SPECIES.

Plate XI, figs. 201–207.

### Odontotermes.

It has been ascertained that the chief tracheæ of the wing-sac in O. badius and O. latericius, fig. 55 (Pl. VI), are the radial, pseudo-medial, and cubital, as in T. natalensis.

### Microtermes sp.

A Microtermes, related to M. albopartitus (*Sjostedt*) found near Pretoria, displays three principal tracheæ, a radial, a medial, and a cubital; the radial bearing a reduced sub-costal. In all the specimens examined the basal attachment of the cubital was far removed from that of the medial and that of the medial well separated from the base of the radial. In this respect and insomuch as the cubital was not found duplicated, this species differs from M. incertus. In one wing-sac, however, the base of the radial stood against that of the medial; this is illustrated by fig. 205 (Pl. XI), a figure which also shows the remarkable loops made by the tracheæ to enter the wing-sac of the more mature nymphs.

### Eutermes (trinervius group).

Numerous studies show that the chief tracheæ of the wing-sac of two or three species are regularly the radial, medial, and cubital. In no case was the cubital or any other found in a duplicated condition. The base of the cubital is always far distant from that of the medial, figs. 203, 204 (Pl. XI). When the nymphs are but moderately grown the three tracheæ stand in the relationship to one another seen in fig. 203; but, later, the cubital and medial are closely applied as they enter the wing-sac, fig. 204. Many wings have been searched for extra principal ribs, but only two were found. In one wing there were two median ribs, the outer simple and running straight to the wing apex, the inner also extending to the wing apex but sending three offsets to the inner margin of the wing. In the other wing, fig. 202, there were also two median ribs, the two being united for a short distance at half the length of the wing; the companion of this wing, fig. 201, presented a normal venation.

Cubitermes bilobatus (*Hav.*).

The chief tracheæ are as in Eutermes (trinervius group). In one case, figs. 206A, B (Pl. XI), a vestigial postcostal was found.

Hamitermes hastatus (*Hav.*).

The chief tracheæ are as with Eutermes (trinervius group). Fig. 207 (Pl. XI) is a sketch from a preparation showing some of the late tracheal developments that occur about the region of the spiracles.

Promirotermes.

Several immature nymphs of two species have been examined and show a radial, medial, and cubital. In one wing-sac there appeared to be a duplication of the medial, fig. 208 (Pl. XI), but it was not possible to trace the basal connections.

## APPENDIX.

### List of Species Referred to in Text.

The localities given are those from which the material examined was obtained.

(1) Hodotermes viator *Latreille.*
Cape Province : Springbok (Klein Namaqualand).

(2) Hodotermes karrooensis *Fuller.*
Cape Province : Victoria West, Middelburg.

(3) Hodotermes transvaalensis *Fuller.*
Transvaal : Pretoria.

(4) Calotermes durbanensis *Haviland.*
Natal : Durban, Winklespruit, Illovo River.
Remarks : In 1898 Haviland described this insect

from specimens of soldiers and workers obtained by James Wylie from trees in the Botanic Gardens, Durban. Some of the nymphs and winged imagos, as well as soldiers and workers which I examined were from the same trees or near-by sources. There is no doubt whatever that the insect to which I have applied Haviland's name is the species he described. It abounds along the seaboard of Natal from the scrub of the beach to well inland.

Sjostedt, who compared Haviland's types with those of Calotermes madagascarensis *Wasman* (1900), placed C. durbanensis as a synonym of Wasman's species. Desneux follows Sjostedt. Holmgren does not mention C. durbanensis in his list of African species. However, he places C. madagascarensis in his sub-genus Proneotermes and places only American species in his Calotermes sensu stricto. It will be obvious from the description of the soldiers which I have given elsewhere[1] and from the wing-studies here presented that the insect can only be placed as a Calotermes sen. str., and, therefore, it can only be discussed as Calotermes durbanensis *Haviland*.

(5) Cryptotermes sp.

Natal: Durban, Winklespruit, Illovo River.

Remarks: Imago resembling C. havilandi (*Sjost.*), soldier differing from C. havilandi (*Sjost.*), as described by Silvestri.

(6) Rhinotermes putorius *Sjost.*

Natal: Durban. Moçambique: Busi River.

(7) Psammotermes allocerus *Silvestri.*

Ovamboland: Namukunde. Cape Province: Van Rhynsdorp, Springbok, Steinkop.

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[1] 'Ann. Nat. Mus.,' p. 451, vol. iii, part 2, 1915.

(8) Termes bellicosus *Smeathman.*
Transvaal: Limpopo River. Moçambique: Busi River.

(9) Termes natalensis *Haviland.*
Transvaal: Pretoria. Natal: Hillcrest.

(10) Odontotermes badius (*Haviland*).
Transvaal: Pretoria.

(11) Odontotermes latericius (*Haviland*).
Transvaal: Pretoria.

(12) Microtermes incertus (*Haviland*).
Transvaal: Pretoria.

(13) Microtermes sp. (near M. albopartitus *Sjostedt*).
Transvaal: Pienaar's River.

(14) Eutermes spp. (trinervius group).
Transvaal: Pretoria, Pienaar's River.

(15) Cubitermes bilobatus (*Har.*).
Transvaal: Pretoria.

(16) Hamitermes hastatus (*Haviland*).
Cape Province: Port Elizabeth.
Hamitermes hastatus (*Har.*)., var. capicola *Silvestri.*
Transvaal: Pretoria.

(17) Promirotermes sp.
Natal: Ixopo.

(18) Microcerotermes spp.
Microcerotermes sp., near M. parvus (*Haviland*).
Transvaal: Pretoria.
Microcerotermes sp., near M. zuluensis *Holmgren.*
Transvaal: Pretoria. Natal: Durban.

## EXPLANATION OF PLATES III—XI,

Illustrating Mr. Claude Fuller's paper, "The Wing Venation and Respiratory System of Certain South African Termites."

### PLATE III.

Fig. 1.—Wing venation: Comstock and Needham's hypothetical type.

Fig. 2.—Hypothetical primitive element of respiratory system; *sp.*, spiracle; *tr.*, tracheal pipe, and its three primary subdivisions: *a*, ascending; *b*, horizontal; *c*, descending trachea.

Fig. 3.—Hypothetical development of ascending trachea (*a* of fig. 2); *aa. aa.*, branches which go to form the dorsal longitudinal trunk.

Fig. 4.—Spiracles VIII, IX, X, with *a.a.a.*, palisade commissures; *Dl. t.*, dorsal longitudinal trunk and its cauda. The visceral tracheæ are omitted. (Diagram.)

Fig. 5.—Hypothetical development of descending tracheæ (*c* of fig. 2) from opposite spiracles, so as to meet and form a ventral commissure.

Fig. 6.—Hypothetical development of horizontal trachea (*b* of fig. 2), so as to link up the spiracles and form the spiracular trunk.

Fig. 7.—Spiracles VIII, IX, X, with the horizontal tracheæ united to the descending trachea of each anterior spiracle, illustrating the indirect primary air route from spiracle to spiracle. (Diagram.)

Fig. 8.—A transverse section of the system.

Fig. 9.—Side view of the system, including spiracles II and III, showing the attachment of the Y-shaped trachea of the second and third legs to the spiracular trunk (*Sp. t.*), and, at *x.x.*, the separation of the tracheæ in the region of the tibiæ.

Fig. 10.—Section of the system about spiracles *X* (the last abdominal), illustrating the paired visceral tracheæ (*x.x.*) from which the palisade commissures seem to arise.

Fig. 11.—Dorsal and lateral parts of the body system, showing the paired dorsal longitudinal trunks, the paired spiracular trunks, the two sets of palisade commissures, and, *x.x.x.x.*, the series of buds upon the dorsal longitudinal trunks.

Fig. 12.—The dorsal longitudinal trunks with the arborescent tracheæ which develop from the buds (*x.x.x.x.* of fig. 11) and which pervade the dome of the body.

Fig. 13.—Ventral parts of the body system, showing the spiracular trunks, the leg tracheæ, and, in solid black, the ten ventral commissures and the cervical commissure which links up the tracheæ of the first pair of legs.

Fig. 14.—The great U-shaped trachea of the head (including spiracles 1) with the bases of the tracheæ attached to it; *l.l.*, of first legs; *m.m.*, of mouth parts; *x.x.*, of the great dorsal tracheæ; *z.z.*, of commissures to dorsal tracheæ. (Diagram.)

Fig. 15.—The frame of the tracheal system of the head, including spiracles I, and showing the U-shaped tracheæ; *x.x.*, the paired dorsals terminating at *y.y.* in the tips of the antennæ; and *z.z.*, the vertical commissures. (Diagram.)

Fig. 16.—The tracheæ of the first pair of legs, including spiracles I and showing *c.c.*, the cervical commissure.

Fig. 17.—The upper region of the respiratory system of the head including a part of the U-shaped trachea; *a.a.*, the tracheæ of the dorso-lateral extensions of the prothorax; *b.b.*, the connections of the dorsal longitudinal trunks with the great dorsal tracheæ of the head; *c.c.*, the tracheæ of the genæ; *d.d.*, the tracheæ of the vertex; *e.e.*, the complexi of the frons. (Diagram.)

Figs. 18 and 19 show the tracheal system of the head, and were designed from a series of camera lucida sketches of cleared preparations of the newly-hatched young of Odontotermes latericius. The various tracheæ may be recognised by comparison of these figures with figs. 14, 15, 17.

Fig. 18.—From below, the nearer or more ventral tracheæ are shown in solid black, the further or more dorsal are shaded. The parts and organs of the head are faintly outlined.

Fig. 19.—From the side (partly from below), showing, in chief, the nearer half of the system; also, the tracheæ of the first legs, part of the first ventral commissure, the Y-shaped tracheæ of the nearer mesothoracic leg, a part of the dorsal longitudinal trunk, and the first palisade trachea of the thorax.

## PLATE IV.

Fig. 20a.—Diagrammatic representations of the tracheal system as seen in the newly-hatched young of T. natalensis, Odontotermes latericius, and Microtermes incertus. On the left, as looked through from above; on the right, as seen when the dorsal longitudinal trunk is thrown aside.

Fig. 20b.—The main system as seen from the side in the cleared preparation of the newly-hatched young of T. natalensis.

Fig. 21a.—The system of the newly-hatched young of Cryptotermes as seen from below. It illustrates the early arrangement of the ventral longitudinal trunks linking up the ventral commissures; the anastomosis of the cervical with the first ventral commissure; the commissure linking up the two ventral trunk tracheæ of the head; the tracheæ of the mouth-parts. (The routes of the paired tracheæ of the labrum are indicated by dotted lines. The palisade commissures and the dorsal longitudinal trunks being the same as those in the metatermite stem, are omitted).

Fig. 21b.—The dorsal tracheæ of the head of Cryptotermes, as arranged in the second stage of their development. (The tracheæ of the vertex and genæ are shown in solid black).

Fig. 21c.—The dorsal tracheæ of the head of Cryptotermes, as seen in the newly-hatched young.

Inset: The mandibles of the nymph of Eutermes *sp.*, showing how both are composed of three well-defined regions.

## PLATE V.

Figs. 22a to 22h.—These figures show the development of the pipes of the thoracic spiracles from enlarged tubes to air-sacs, figs. 22a to 22e being of the first pair, and figs. 22f, g, h of the second pair. All are proportionately enlarged except fig. 22e, which is drawn upon a smaller scale. The conditions represented by figs. 22f and g accompany the conditions of the first spiracle in figs. 22a to d; fig. 22h of the second spiracle accompanies the condition seen in fig. 22e of the first spiracle. All figures are from camera lucida sketches of nymphs of Microtermes incertus. The bases of the tracheæ shown are in figs. 22a to 22e those of: (1) The dorsal trachea of the head which terminates in the tip of the antenna; (2) the stem of the U-shaped ventral trachea of the head which bears the tracheæ of the mouth-parts; (3) the trachea of the first leg; (4) the ventral commissure of spiracles I; (5) the trachea to the second spiracle. In figs. 22f, g, h they are the bases of (1) the trachea to the first spiracle; (1a) the trachea to the third (or first abdominal) spiracle; (3) the ventral commissure of spiracles II.

Figs. 23a, b, c.—These figures illustrate the apparent arrangement of the abdominal series of spiracles (spiracles III to X as seen from within) in the newly-hatched young of T. natalensis and T. latericius. The features shown are: (1) The circular pore or fixed opening in the cuticle; (2) the atrium; (2a) the vestigial resister; (3) the lever; (4) the epitrachelos; (5) the trachelos; (6) the tracheal pipe; (*oc. m.*) the occlusor; (*ex. m.*) the extensor muscle.

Figs. 23a and b show the spiracle open and 23c closed. In 23b the epitrachelos is removed to show (in solid black) the side opening in the organ through which the air passes into the epitrachelos. In 23C the epitrachelos is seen closed by the pinching of the lever against the resister (more or less diagrammatic).

Figs. 24A and 24B.—The abdominl spiracle in the second stage of development (T. natalensis). Fig. 24A, viewed from within; fig. 24B, the outer aspect. Both figures illustrate the development of the resister and its hiatus, the extension of the trachelos, and the disappearance of the epitrachelos.

Figs. 25A, B, C.—Sections of the lever, showing the hypothetical development or change from an ascidium to a plate. (Diagrams.)

Fig. 26A.—A section of the base of the atrium, showing how, in the second stage spiracle, the resister protrudes into the lumen. (Diagram.)

Fig. 26B.—An interior view of the resister, showing the hiatus and bulge. (Diagram.)

Figs. 27A and B.—The resister and lever, showing dorsal strap or fulcrum connecting the two; fig. 27A, viewed from within; fig. 27B, the outer aspect. (Diagrams.)

Figs. 28A and B.—The resister and lever with muscle attached; fig. 28A, attitude when the lumen is open; fig. 28B, when the lumen is closed. (Diagrams.)

Figs. 29A and B.—Dorsal aspect of spiracles; fig. 29A, showing the lever drawn against the resister and the lumen closed; fig. 29B, showing the relationship of lever to resister when the lumen is open. (Diagrams.)

Fig. 30.—Abdominal spiracle in transition between second and third stages (T. natalensis). View from within, showing *nr.*, a new rim developing behind the rim of the pore (*pr.*), and *ch.*, the large chin-plate that develops on the side of the atrium against the resister.

Figs. 31A, B, C.—Abdominal spiracle of the third stage (T. natalensis). Fig. 31A, viewed from within, showing (1) the shortening of the atrium; (2) the tympanic chin-plate; (3) the compressed resister; (4) the hexagonal, tessellated trachelos pinched against the resister by (5) the lever. The position of the lever, when open, is also indicated. Fig. 31B, outer aspect; a diagram representing the throwing off of the pore and atrium, or the transition of the spiracle from the third to fourth stage. (Compare the left-hand part of the diagram with fig. 34.) Fig. 31C, diagram representing the same, but viewed from above.

Fig. 32.—Spiracle III (the first abdominal) of T. natalensis, female. External aspect viewed from the side, illustrating a distinct transformation to the bivalvular form in which *R.* the resister is

reduced to form a narrow edge to *C.*, the tympanic chin-plate, and *L.*, the lever has developed a strong thumb-like projection. The trachelos (*m. tr.*) is also seen within the open mouth of the spiracle. (The cuticle is not indicated.)

Fig. 33.—Spiracle IV (the second abdominal) of T. natalensis, female: not so decidedly transformed as spiracle III. Lettering as for fig. 32.

Fig. 34.—Spiracle X (the last abdominal) of T. natalensis, female; still less decidedly transformed. Lettering as for fig. 32.

Fig. 35.—Abdominal spiracle of Hodotermes, female, as seen from the outside, showing the two thumb-like projections to which the muscles are attached. Lettering as for fig. 32.

Figs. 36a, b, c.—The abdominal spiracles of Hodotermes, male, fig. 36a, from without; fig. 36b, from within, open; fig. 36c, from within, closed.

Fig. 37.—The rim (from within) of the spiracle of the second stage, T. natalensis (fig. 24a), showing the hexagonal (tessellated) framework.

Figs. 38a, b, c.—The thoracic spiracles of T. swaziæ, fig. 38a, the second; fig. 38b, the first; fig. 38c, the second disrupted to separate the occlusor from the extensor muscle drawn on a much smaller scale than 38a.

Fig. 39.—The tracheæ of the femur in the half-grown nymph of T. natalensis.

Figs. 40, 41, 42, 43a and 43b, progressive stages in the development of the abdominal pipes of the female nymph of T. natalensis. Fig. 40, the distension of the pipes; figs. 41 and 42, two stages of the growth of the multitude of dichotomising tracheæ from the pipes; fig. 41, *p. com.*, palisade commissure; *d. tr.*, dorsal trunk; *v. com.*, ventral commissure; *sp. tr.*, spiracular trunk. Fig. 43a, an outer aspect of the tracheal arrangement about the abdominal spiracles of an almost mature nymph, showing *sp. t.*, the spiracular trunk; *vc. vc.*, ventral commissures; *pc. pc.*, palisade commissures; *O. C.*, the ovarian chord embraced by two of the tracheal bunches. Fig. 43b, the inner aspect of the arrangement represented by fig. 43a, showing two perpendicular and one oblique muscle and the peristaltic ribbon.

Fig. 44.—A side view of an abdominal spiracle of the adult female (T. natalensis), showing *L.*, the lever; *trl.*, the trachelos, and some of the many dichotomising tracheæ that open into the cup formed by the trachelos.

Fig. 45a.—A part of a disrupted spiracle of the distended female (queen) of Odontotermes badius, showing how the tracheæ open freely into the disruption.

FIG. 45B.—Outside aspect of the disrupted spiracle of the distended female of T. natalensis, showing the mouths of the tracheæ and the tracheate character of the disruption.

FIG. 46.—Diagram of the tracheal stem (Metatermite) of the head and thorax.

FIG. 47.—Diagram of the tracheal stem (Metatermite) to illustrate homologies.

FIG. 48.—Diagram of a section of the tracheal stem of the Calotermite type, to show that the wing tracheæ originate from the spiracular trunk; both the dorsal longitudinal and the ventral longitudinal tracheæ being present.

## PLATE VI.

FIG. 49.—Thorax of a young Cryptotermes nymph, illustrating the lateral bulging out of the spiracular trunk (shown in solid black) within the meso- and metathorax.

FIGS. 50A, B, C.—The genesis of a trachea bud in three stages of development; as found on a series of tracheal pipes in the abdomen of a Calotermes nymph.

FIG. 51.—The buds of wing tracheæ.

FIG. 52.—Clavate tubercles of wing tracheæ.

FIG. 53.—Conical tubercles of wing tracheæ.

FIG. 54.—The sub-apical growth of tracheæ from tubercles.

FIG. 55.—Wing-sac of very young nymph of Odontotermes latericius with a simple conical bud (the radial) and a furcate bud (the cubital).

FIG. 56.—The bud of the post-costal (*Pst. c.*) on base of radial (*R.*). (Cryptotermes.)

FIG. 57.—The vermiform bud of sub-costal (*Sc.*) on radial. (Cryptotermes.)

FIG. 58.—Early form of anal (*A.*) on cubital (*Cu.*). (Cryptotermes.)

FIG. 59.—Fore and hind wing-sacs of Cryptotermes, showing the early form of the six principal tracheæ.

FIG. 60.—The lateral tracheæ of the thorax of Cryptotermes; *a.a.a.*, dorsal longitudinal; *b.f.b.*, spiracular trunk; *c.*, first spiracle of abdomen; *d.*, second spiracle of thorax; *e.e.*, arms of leg tracheæ; *g.*, stem of leg trachea.

FIG. 61.—Wing-sac of full-grown nymph (T. natalensis), illustrating the beginning of the growth and folding of the final wing, accompanied by the displacement and coiling up of the tracheæ. Tracheæ in focus

shown in solid black, those further away are shaded; the thickening of the margin is also indicated; *c.*, costal thickening; *R.*, radial; *Ps. M.*, pseudo-medial; *Cu.*, cubital.

Figs. 62a and b.—These figures illustrate the migration of a trachea from the thickening that forms about it.

Figs. 63a and b.—The figures illustrate the movement of the cubital offsets from thickenings and the forming of new bands about them in their new positions.

Fig. 64.—The wing of T. natalensis as it appears before and after the last ecdysis. Viewed from below.

Figs. 65a to 65k.—The various stages of the unfolding of the wing of T. natalensis (side views; the diagrams are all of the same relative enlargement). Fig. 65a represents the condition shown in fig. 64; figs. 65b, c, d, e, the conditions seen in figs. 67a, b. Fig. 65k represents a fully expanded wing.

Fig. 66.—T. natalensis; imago with wings unfolding.

Figs. 67a, b, c, d.—T. natalensis; wings in various stages of unfolding; a, b, c, from above; d, from below.

Fig. 68.—Calotermes durbanensis; basal half of freshly unfolded and transparent wing, showing the thickenings then present and (in solid black) the lumina; *x.*, the cross-rib, with lumen, connecting post-costa to costa.

Fig. 69.—Diagram representing the stretched-out condition of the spiral of the lumina of fig. 68.

Figs. 70a and b.—Hodotermes karrooensis; fig. 70a, wing-stump and base of lamina of fore wing; fig. 70b, the same of hind wing.

Fig. 71.—Hodotermes viator; illustrating the abnormal position of pseudo-media (in solid black) in a particular hind wing.

Figs. 72a and b.—H. viator; illustrating the abnormal duplication of the sub-costa (in solid black).

Fig. 73.—H. viator; illustrating the deep furcation of the sub-costa (in solid black).

Fig. 74.—H. viator; illustrating the deep furcation of the post-costa (in solid black).

Fig. 75.—Hodotermes transvaalensis; portion of wing-base illustrating the absence of a pseudo-media.

Fig. 76.—H. transvaalensis; illustrating the duplication of the pseudo-media (in solid black).

Fig. 77.—Hodotermes viator; illustrating an abnormally well-branched condition of the sub-costa (in solid black).

## PLATE VII.

FIG. 78.—Hodotermes viator; wing-sac of nearly mature nymph with the detail of the tracheæ; *x*., the trachea preceding the cross-rib from post-costa to costa. Post-costal independent.

FIG. 79.—H. viator; an abnormally reduced inner cubital (*Cu.*).

FIGS. 80, 81, 82, 83.—H. viator; the cardinal trachea and the basal connections of the tracheæ of the wing-sac, illustrating abnormal developments. Fig. 80 (? M, in solid black), an extra trachea, probably the medial, originating from the base of (*ps.-m.*) the outer cubital (or pseudo-medial). Fig. 81, a deeply furcate (or duplicated) post-costal (in solid black). Fig. 82, an extra principal trachea (in solid black) entering the wing-sac and associated with the radial. Fig. 83, the pseudo-medial, cubital, and anal arising almost independently.

FIGS. 84A, B, C, D.—H. viator, normal wings; fig. 84A, fore wing; figs. 84B, C, D, hind wings.

FIGS. 85 and 86.—Calotermes durbanensis; wing-stump and base of lamina; fig. 85, of fore wing; fig. 86, of hind wing.

FIG. 87.—C. durbanensis; part of lamina of hind wing with (in solid black) an independent post-costa.

FIGS. 88–103B represent the development and abnormalities of the tracheæ of the wing-sac of C. durbanensis. Figs. 88–97, 101A and 102A are more or less in proportion.

FIGS. 88–94.—These illustrate the normal progressive development of the tracheæ, commencing from the hinder wing-sac of fig. 88. In fig. 88 the more advanced condition of the tracheæ of the meso-thoracic wing-sac (of a moderately young nymph) is well-marked. In fig. 91 the branch to the sub-costal is an unusual feature. In fig. 94 is shown that extension of the principals, and that growth from these of many small tracheæ, to be found in the wing-sac of a nymph, in the last stadium, prior to the development of the final wing.

FIG. 95.—An abnormal medial (in solid black); the trachea has two strong outer branches which cross one another and extend to the apex of the sac.

FIG. 96.—A medial (in solid black) taking an abnormal path in crossing the cubital, and extending to the inner margin of the sac.

FIG. 97.—An abnormal medial (in solid black) duplicated from the cardinal, the two tracheæ crossing.

FIGS. 98A and B.—Illustrating the basal connection of an extra principal trachea with the medial. In fig. 98A the extra trachea is shown in solid black; in fig. 98B the junction of the two is illustrated.

FIGS. 99A and B.—Illustrating the basal connection of an extra principal trachea with the cubital. In fig. 99A the extra trachea is shown in solid black; in fig. 99B the attachment of it and the anal to the cubital is illustrated.

FIG. 100.—Illustrating the basal arrangement of the tracheæ of a wing-sac in which the post-costal and cubital were found duplicated.

FIG. 101A.—A wing-sac in the same condition of development as that shown in fig. 94, with an abnormal scheme due to the displacement and extraordinary development of a furcate anal (in solid black). Other abnormal features are: (1) The absence of the sub-costal; (2) the reduced and branchless condition of the radial; (3) the branched condition and displacement of the medial; (4) the large outer branches of the cubital.

FIG. 101B.—The basal connection of the furcate anal of fig. 101A with the cubital is shown.

FIG. 102A.—Wing-sac in the same condition of development as that shown in fig. 94, with an abnormal scheme due to the presence of three extra principal trachea, the sub-costal, medial, and cubital all being duplicated.

FIG. 102B.—The basal connection of the duplicated sub-costal with the radial is shown.

FIGS. 103A and B.—These illustrate the unusual development of an inner branch upon the base of the radial. Fig. 103B shows the basal part of this unusual branch.

## PLATE VIII.

### Calotermes durbanensis.

Wings with normal and sub-normal venation.

FIG. 104.—Fore; normal; *M.* with furcate tip and no basal branches; *R.* with cross-branch to *Sc.*

FIG. 105.—Hind; normal; *M.* simple, with three short basal branches.

FIG. 106.—Hind; normal; *M.* unusually subdivided.

FIG. 107.—Fore; normal; *M.* somewhat deeply furcate, with many cross-branches between *M.* and *R.*; offsets of *R.* furcate.

FIG. 108.—Fore; normal; with *M.* faintly furcate and with two-hooked basal branches.

FIG. 109.—Hind; normal; *M.* simple, with three basal branches; *R.* with cross-branch to *Sc.*

FIG. 110.—Hind; normal; *M.* furcate without basal branches.

FIG. 111.—Hind; normal; M. furcate with two curved basal branches.

FIG. 112.—Hind; normal; *M.* with an uncinate basal branch.

Fig. 113.—Fore; sub-normal; *M.* and *Cu.* connected by a cross-branch; *M.* with sinuate basal branches (cf. fig. 119).

Fig. 114.—Fore; normal; *M.* simple with two long basal branches, forming cells.

Wings with sub-normal and abnormal venation.

Fig. 115.—Hind; abnormal; *M.* simple but approximated to *R.*

Fig. 116.—Hind; sub-normal; *M.* deeply furcate and subdivided.

Fig. 117.—Hind; abnormal; *M.* duplicated with both tips strongly incurved.

Fig. 118.—Fore; abnormal; *M.* and *Cu.* fused (probably due to crossing of tracheæ *M.* and *Cu.*).

Fig. 119.—Fore; sub-normal; *M.* and *Cu.* fused; ridges between cubitus offsets recording movement of pre-existing tracheæ. (Compare with fig. 113.)

Fig. 120.—Hind; abnormal; *M.* deeply furcate or duplicated; *M.* and *Cu.* connected by cross-branch (probably due to crossing of branches of trachea *M.* and to crossing of trachea *Cu.* by these branches).

Fig 121.—Hind; abnormal.

Fig. 122.—Hind; abnormal; *M.* duplicated in basal half of wing.

Fig. 123.—Fore; abnormal; *Sc.* furcate; *M.* reduced and united to *R.* (probably due to a duplication of trachea *M.* accompanied by reduction); *Cu.* highly developed and connected to *R.* by cross-branches characteristic of *M.*

## PLATE IX.

### Calotermes durbanensis.

Wings with abnormal venation.

Fig. 124.—Fore; abnormal; probably owing to duplication of cubital trachea; *R.* with cross-branch to *Sc.*

Fig. 125.—Fore; very abnormal; condition not readily explained, but due to tracheal tangle.

Fig. 126.—Hind; abnormal on account of independents between cubitus offsets; *M.* subdivided at apex, with a long, bicurvate cross-branch to *R.* at base.

Fig. 127.—Fore; abnormal; *M.* furcate, crossing *Cu.*, with an uncinate branch at base.

Fig. 128.—Fore; abnormal; *M.* deeply furcate; condition due to crossing of tracheæ.

Fig. 129.—Hind; abnormal; *M.* reduced and fused to *R.*; *Cu.* with cross-branches to *R.*, characteristic of *M.*

FIG. 130.—Fore; abnormal; *M.* furcate; *Cu.* crossing branches of *M.* and fusing with *R.*

FIG. 131.—Hind; abnormal; probably owing to a duplication of trachea *Cu.*, the extra trachea becoming associated with *M.*; or, possibly, to a duplication of trachea *M.* and a high development causing a reduction of *Cu.*

FIG. 133.—Fore; abnormal; *M.* duplicated, both stems reduced and fused to *R.*

FIG. 134.—Fore; abnormal; *M.* unusually developed.

## PLATE IX.

### Cryptotermes, *sp.*

### Wings and wing-sac tracheæ.

FIGS. 135A and B.—Wing-stump and base of lamina; fig. 135A, fore wing; fig. 135B, hind wing.

FIG. 136.—Wing-sac of very young nymph, presenting three principal tracheæ (*R.*, *M.*, *Cu.*), which are more or less straight and parallel.

FIG. 137.—Wing-sacs of young nymph, more advanced than that illustrated by fig. 136, presenting five principal tracheæ (*P. sc.*, *C.*, *Sc.*, *R.*, *M.*, *Cu.*).

FIG. 138.—Wing-sacs of young nymph, more advanced than that illustrated by fig. 137, illustrating the development of offsets from *R.* and *Cu.* and the delayed development of the anal.

FIGS. 139A to G.—Diagrams illustrating some of the varied developments of the medial. A, common form; B, medial entwining radial; C, medial departing from radial after becoming applied to it; D, medial with a straight, sector-like branch; E, medial with a sinuate sector; F, medial with a reduced sector; G, sector of medial with two fine branches.

FIG. 140.—Dorsal aspect of cardinal and bases of tracheæ of wing-sac.

FIG. 141.—Wing-sac of a fully-grown nymph with full complement of tracheæ.

FIG. 142.—Apex of wing-sac of a fully-grown nymph, illustrating (1) how the principals extend; (2) how the offsets of the cubital dichotomise and recurve into the field of the wing-sac.

## PLATE X.

### Cryptotermes, *sp.*

FIG. 143.—Normal fore wing; *M.* with sector-like branch to apex, with cross-branches between *M.* and *R.* and between *M.* and *Cu.*

Fig. 144.—Normal fore wing; *Cu.* strongly developed, with outer branches to *R.*

Fig. 145.—Normal hind wing, with independent rib from apex, probably a disconnected sector-like branch of *M.*; the tip of the medial trachea probably left the radial as in fig. 139c, giving rise to the short inner branch of *R.*

Fig. 146.—Normal hind wing; sector-like branch of *M.* subdivided; two offsets of *Cu.* incurved.

Fig. 147.—Normal fore wing; *Cu.* strongly developed, but on lines quite different from those in fig. 144.

Fig. 148.—Abnormal hind wing; *M.* not attached to *R.*; with an extra rib applied, in part, to *M.*

Fig. 149.—Abnormal hind wing, probably due to a duplication of the cubital trachea.

Fig. 150.—Abnormal hind wing; *M.* duplicated; *M.* not attached to *R.*

Fig. 151.—Abnormal hind wing; extra rib furcate and clearly defined.

Fig. 152.—Abnormal hind wing; *M.* attached at base to *Cu.* instead of to *R.*, with two well-defined, independent ribs between offsets of *Cu.*

Fig. 153.—Cardinal and bases of wing-sac tracheæ, naturally arranged, showing an extra trachea on the base of the radial, which assumes the rôle of an anal after applying itself to the cubital.

Fig. 154.—Illustrating an abnormal development of the tracheæ of the wing-sac; the medial with (1) a well-developed branch crossing the cubital; (2) a branch crossing the radial; (3) a well-developed inner branch.

### Rhinotermes putorius.

Figs. 155 and 156.—Rhinotermes putorius; fig. 155, fore wing; fig. 156, hind wing.

Figs. 157 and 158.—R. putorius; wing-stump and base of lamina; fig. 157, fore wing; fig. 158, hind wing.

Fig. 159.—R. putorius; wing-sacs of very young nymph, illustrating the development of the tracheæ.

Figs. 160 to 163.—R. putorius; the tracheæ of four wing-sacs of one very young nymph, showing four sufficiently different developments.

Fig. 164.—R. putorius; the normal tracheation of the wing-sac of a nearly mature nymph.

Fig. 165.—R. putorius; the abnormal tracheation of the wing-sac of a nearly mature nymph, exhibiting an extra principal trachea.

Fig. 166.—R. putorius; the cardinal and bases of the tracheæ illustrated in fig. 165.

### Psammotermes allocerus.

Fig. 167.—Fore wing with a well-developed media.

Fig. 168.—Hind wing with a well-developed media.

Figs. 169 to 173.—A series of wings in which the media is absent and the cubitus variously developed.

## PLATE XI.

### Termes natalensis.

Fig. 174.—Normal wing; *R.* with one sector.

Fig. 175.—Normal wing; *R.* with three sectors.

Fig. 176.—Wing-sac showing tracheation displayed prior to final ecdysis.

Fig. 177.—A part of fig. 176; more enlarged, illustrating the marginal thickening.

Fig. 178.—A part of fig. 176; greatly enlarged, illustrating the subdivision and spreading of the cubital offsets on approaching the marginal thickening.

Fig. 179.—Cardinal trachea of mesothorax, showing the genesis of the trachea of the wing-sac.

Fig. 180.—Cardinal trachea of metathorax, showing a more advanced condition than that of the mesothorax (fig. 179).

Fig. 181.—Wing-sacs of very young nymph, illustrating early form of principals; a post-costal is present in the anterior organ only.

Figs. 182 to 187.—The cardinal trachea and the basal attachments of the principal tracheæ of the wing-sac as seen in fairly mature nymphs.

Fig. 182.—The post-costal has an independent base between that of the radial and the leg trachea; the anal is well-developed and directed into the thoracic cavity.

Fig. 183.—The post-costal emerges from the base of a bunch of tracheæ which lies well in front of the leg trachea; the base of the radial is fused with that of the cubital; the anal is missing.

Fig. 184.—The post-costal arises from the stock of the radial (as in Hodo-, Calo-, and Cryptotermes); the anal is atrophied.

Fig. 185.—The post-costal is attached similarly to the case illustrated by fig. 184, but is subdivided; the base of the radial is more or less as in the case illustrated by fig. 183; here also the anal is missing.

Fig. 186.—The post-costal is as in figs. 183 and 187; the anal is present but not highly developed.

Fig. 187.—The post-costal as in figs. 183 and 186; the anal has an independent attachment to the cardinal; an atrophied trachea (probably the medial) arises from the base of the cubital.

### Microtermes incertus.

Figs. 188 and 189.—Normal fore wing and hind wing, showing struts between costa and radius.

Fig. 190.—Normal hind wing, with sector to radius.

Fig. 191.—Abnormal fore wing, with *M.* and *Ps. M.* both present.

Figs. 192 and 193.—Abnormal fore wings with *M.* present, reduced and attached to *R.*

Fig. 194.—Abnormal fore wing; *Ps. M.* attached to *R.*

Figs. 195, 196, 197.—The cardinal trachea, with buds of wing-sac tracheæ developing.

Fig. 198.—Wing-sacs of a very young nymph, showing early condition of tracheation.

Fig. 199.—Wing-sac of a young nymph in which were the present *Pst. C.*, *Sc.*, and anal.

Fig. 200.—Cardinal trachea and bases of principals, showing an extra trachea (an independent medial) in the presence of a duplicated cubital.

### Eutermes (trinervius group).

Fig. 201.—Normal fore wing.

Fig. 202.—Abnormal fore wing (the companion of fig. 201) with a duplicated media.

Fig. 203.—Cardinal and bases of principal tracheæ of wing-sac, as seen in young nymphs.

Fig. 204.—Cardinal and bases of principal tracheæ of wing-sac, as seen in older nymphs; *M.* and *Cu.* closely applied.

### Microtermes *sp.*

Fig. 205.—The cardinal and bases of principal tracheæ of wing-sac; the root of *R.* abnormally close to that of *M.*

### Cubitermes bilobatus.

Fig. 206a.—The cardinal with bases of principal tracheæ of wing-sac; the radial bearing (abnormally) a vestigial post-costal.

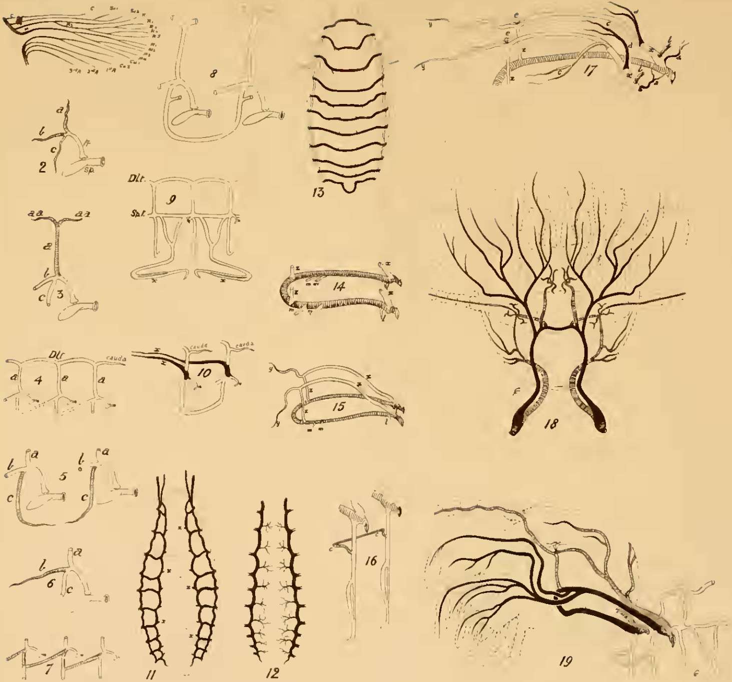
Fig. 206b.—An enlarged view of the vestigial post-costal of fig. 206a.

### Hamitermes hastatus.

Fig. 207.—The cardinal and bases of the principal tracheæ of wing-sac; also the bases of the leg trachea and of the bunches of thoracic tracheæ.

### Promirotermes *sp.*

Fig. 208.—Wing-sac with three normal tracheæ (in solid block) and an extra trachea (? medial), also an unusually large branch to the cubital.



TERMITE TRACHEAL SYSTEM

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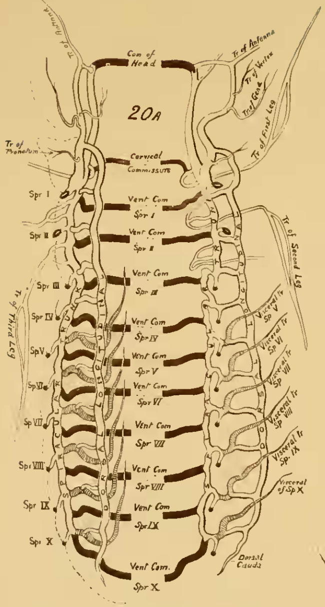

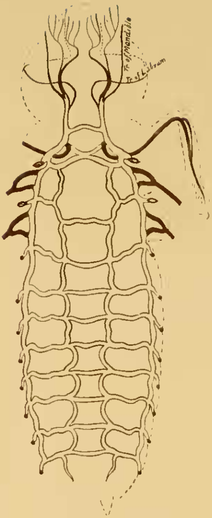

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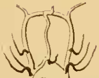

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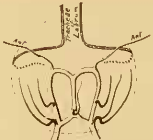

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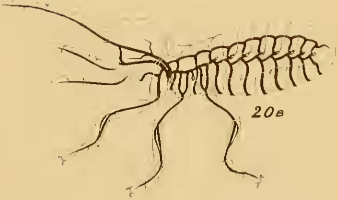

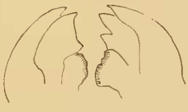

Mandibles of Eutermes

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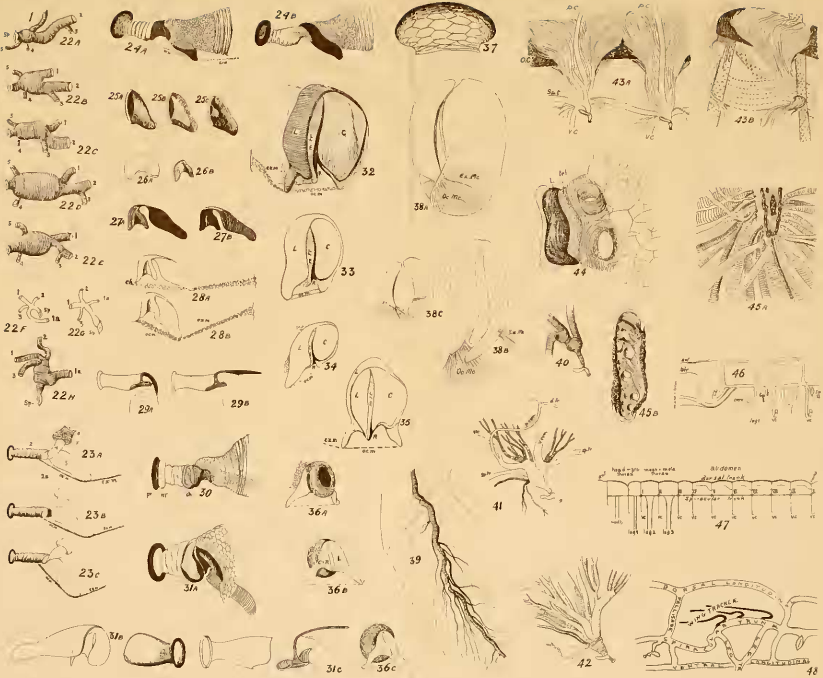

TERMITE SPIRACLES AND WING TRACHEÆ

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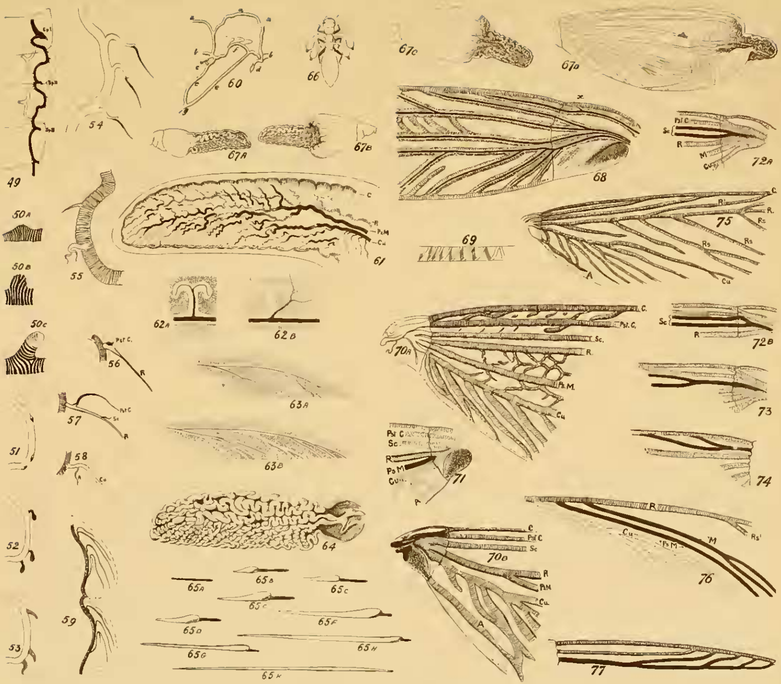
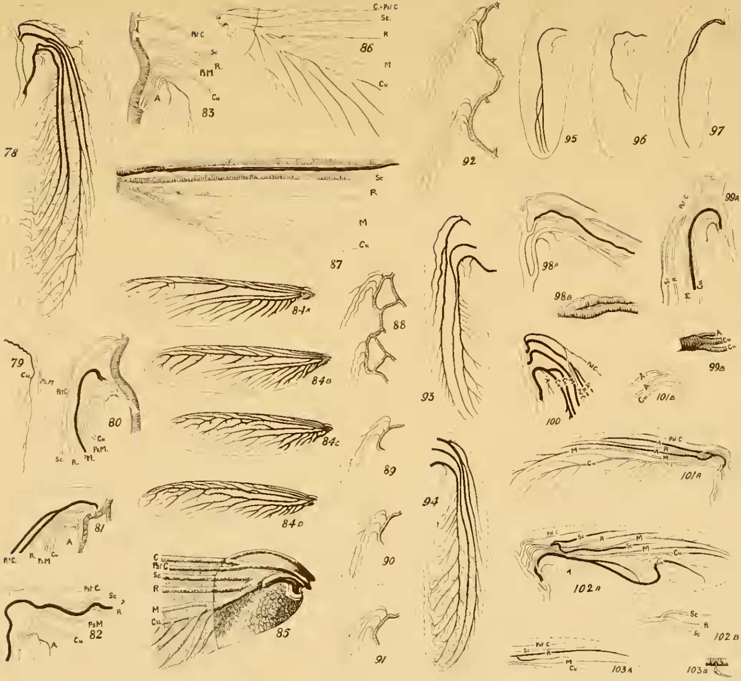


TERMITE WING TRACHEÆ UNFOLDING OF WING WING VENATION



Wing Tracheæ and Venation of Hodotermes viator (Figs. 78–84) and Calotermes durbanensis (Figs. 85–103)

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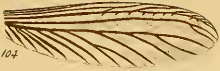
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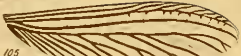
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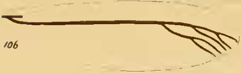
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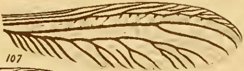
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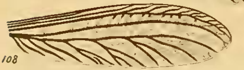
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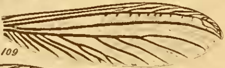
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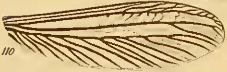
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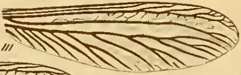
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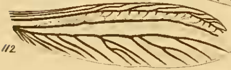
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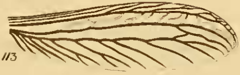
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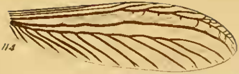
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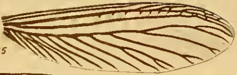
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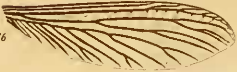
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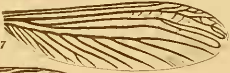
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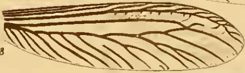
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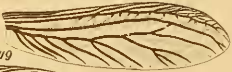
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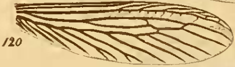
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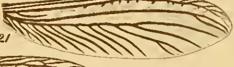
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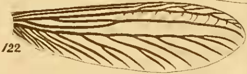
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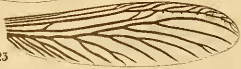
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WING VENATION OF CALOTERMES DURBANENSIS.

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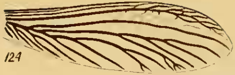
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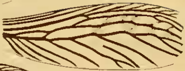
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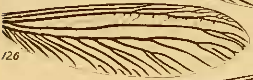
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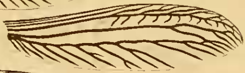
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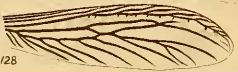
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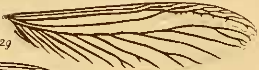
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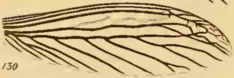
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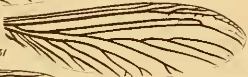
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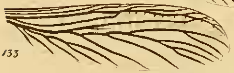
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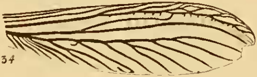
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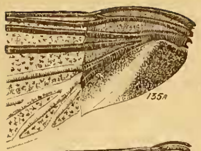
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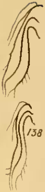
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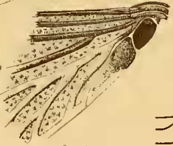
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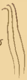
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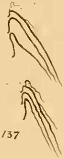
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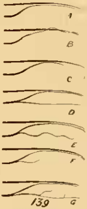

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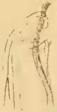
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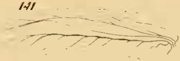
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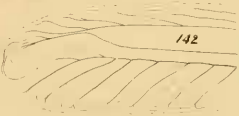
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CALOTERMES DURBANENSIS (FIGS 124 134) CRYPTOTERMES SP (FIGS 135 142)

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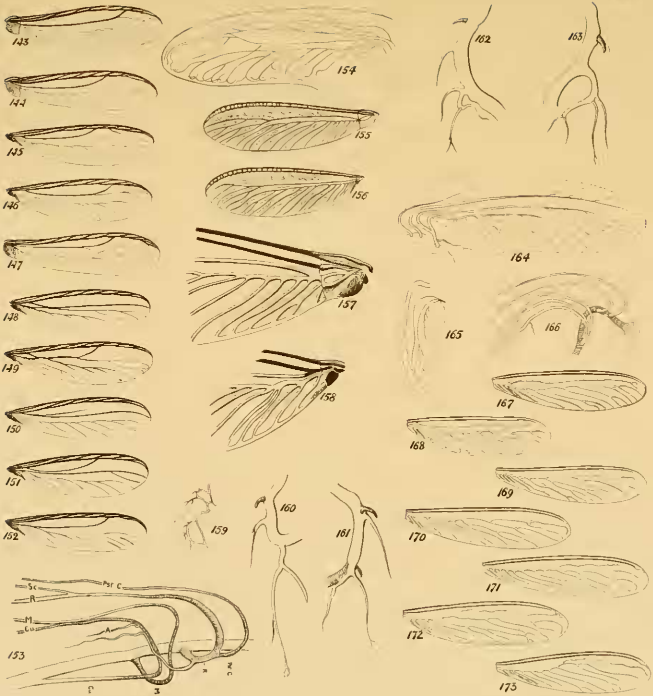

Cryptotermes sp (figs. 135–154), Rhinotermes putorius (figs. 155 166), Psammotermes allocerus (figs. 167 173).

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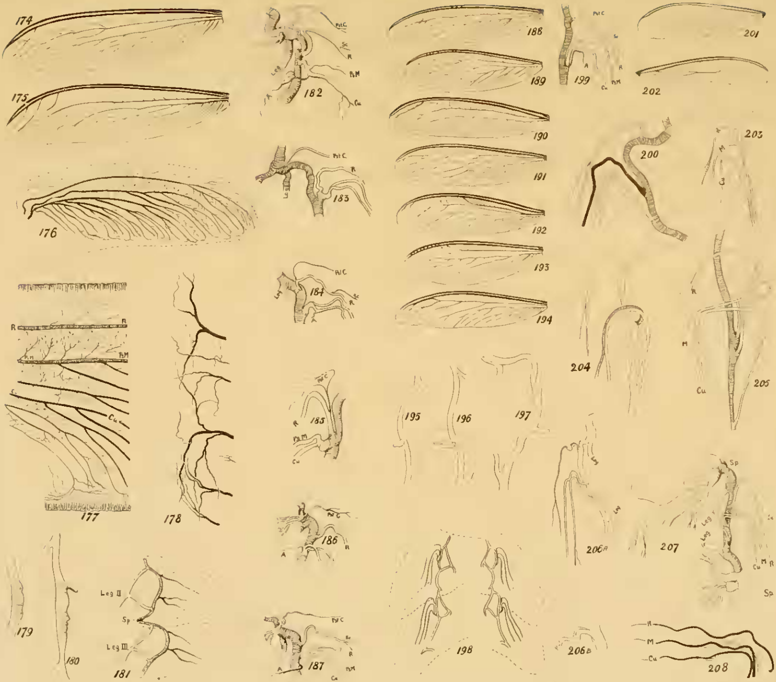

Termes natalensis, (figs 174-187), Microtermes incertus (figs. 188-200), Eutermes (figs 201 204), Microtermes sp (fig 205)
Cubitermes bilobatus (fig 206), Hamitermes hastatus (fig 207), Promirotermes sp (fig 208)

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